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Date of this issue 20 August 1986



## Rediscovery and Identity of the Holotype of *Helminthoglypta diabloensis* (Cooper) (Gastropoda: Pulmonata)

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**Abstract.**—The holotype of *Helix diabloensis* Cooper 1869, thought to have been lost, has been rediscovered and returned to the type collection of the University of California (Berkeley) Museum of Paleontology.

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The only type specimen of the Californian land snail *Helix diabloensis* Cooper 1869 has long been considered lost (Pilsbry 1927, 1939; Coan 1982). The species was originally characterized, without being named, in the following passage:

“There is a single specimen of *Helix* in the State Collection, supposed to have been obtained in the Mount Diablo Range by Prof. Brewer, which closely resembles the small form of *H. sequoicola* in shape, but being nearly bleached is too imperfect to describe minutely, though very likely a new species. It is remarkable for having seven whorls, while the former and *H. mormonum* of the same size have but six; it is also less compressed than the latter, and the umbilicus is less covered. The color where remaining is shining gamboge yellow (faded?) with a *single* very narrow band *above* the middle, not showing the pale band on each side of it that is so marked in others of the group. The sculpture seems to have been very *slightly* malleated, and with the faint lines of growth cut by smooth depressed waved grooves transversely, and thus obliquely to the sutures (while those of *H. traskii* are parallel). Diameter maj. 0.95; alt. 0.40 inch” (Cooper 1866:260-261).

Cooper (1867:332-333) referred to this unique specimen as possibly “a hybrid between [*Monadenia*] *mormonum* and [*Helminthoglypta nickliniana*] *ramentosa*.” Two years later Cooper (1869:221) proposed the name *Helix diabloensis* with reference to the original passage; the name is available as of this citation, and the holotype is the specimen mentioned above.

Cooper (1872) presented a formal description (as “*Lisinoe diabloensis*. Cp. n. s.”) and figures based on new material collected by L. G. Yates at Cedar Mountain, southeastern Alameda County. The previous citations were listed in synonymy. He also tentatively referred specimens “said to come from San Luis Obispo” to the same species. The present location of these specimens and those from Cedar Mountain is unknown, but they have no bearing on the typologic definition of the taxon.

On the basis of these descriptions, and specimens sent out by Cooper, subsequent authors (Binney 1885; Pilsbry 1927, 1939; Ingram and Lotz 1950) inter-





Figs. 1-3. *Helminthoglypta diabloensis* (Cooper), holotype, UCMP 37536. Top, apertural, and basal views,  $\times 1.5$ .

preted *H. diabloensis* as one of the common species of *Helminthoglypta* Ancey 1887 of the hills between San Francisco Bay and the San Joaquin Valley. The *H. diabloensis* of authors has a depressed-trochoid shell of from six to seven closely coiled whorls, a well-impressed suture, and an umbilicus generally less than half covered by the expanded inner lip. The sculpture of fine, crowded rugae obliquely intersected by forwardly descending riblets gives the surface a distinctively silky luster. It is usually found in leaf litter in wooded areas, typically along stream courses. Pilsbry (1939) reported a range extending through the inner Coast Ranges from Colusa, Napa, and Yolo counties south to Pacheco Pass, Santa Clara County. However, several workers including the authors have collected it as far south as the vicinity of Panoche Pass, San Benito County.

The holotype was collected by William H. Brewer, probably during his geologic reconnaissance of the southern Coast Ranges of California in July 1861 (Brewer 1930), but the type locality is not known. Cooper variously stated that it came from "the Mount Diablo Range" (1866); Mount Diablo (1867); "near New Idria," San Benito County, where Brewer visited the quicksilver mines of the Diablo Range (1869); "east of Mount Diablo" (1872); or on the east slope of Mount Diablo (1887). Pilsbry (1939:105) concluded that Brewer "probably picked it up in Contra Costa or in Alameda county."

The holotype was rediscovered in February 1985, during the transfer of the mollusk collection of the late S. Stillman Berry from his house in Redlands, California, to the Santa Barbara Museum of Natural History (Hochberg 1985). Dr. Clyde F. E. Roper of the Smithsonian Institution found it along with other material from the University of California in a section of the collection containing mostly cephalopods. The voluminous Berry correspondence has not yet been sorted through, but the loan transaction probably dates from before 1927 when Pilsbry reported the type specimen lost. Berry was actively publishing on Californian land mollusks around this time.

The specimen (Figs. 1-3) was immediately recognizable as the holotype. Printed in ink on the shoulder of the body whorl, in what may be Cooper's hand, is "Lysinoe Diabloensis Cp" and on the body whorl in front of the aperture, "type." The specimen conforms well to Cooper's (1866) original description quoted above. It was accompanied by a hand-lettered label typical of those formerly used by the University of California (Berkeley) Museum of Paleontology (UCMP) reading: "Helix (Lysinoe) diabloensis/Cpr./San Luis Obispo/Dr. Newcomb/2421/(Type)." A second, printed label of the Palaeontological Collections of the University of



California, probably of later date, bears the typed data "Epiphragmophora traski var./San Luis Obispo."

When Cooper examined the shell it was in the collection of the California Geological Survey. This collection was transferred to the University of California on dissolution of the survey in the late 1800's. The specimen has now been deposited in the UCMP type collection where it is No. 37536.

The shell is solid, umbilicate, depressed-trochoid with conic spire; the base is moderately inflated, somewhat excavated around the umbilicus. The initial whorls are eroded smooth, with faint traces of malleation remaining. Fine radial rugae congruent with lines of growth become apparent on the third whorl; from about the fifth whorl on, these are intersected by a set of forwardly descending riblets, lower than the rugae but higher than their interspaces, cutting the latter into a series of radially elongated pits. On the last whorl the descending riblets split and fuse irregularly, producing a malleated surface. The base is smooth except for erosional pitting, with rugae and malleation nearly obsolete. Around the umbilicus there are faintly impressed fine spiral striae and traces of low, weak papillation. The shell is white with smooth, yellowish brown periostracum preserved on the last half of the body whorl. The shoulder bears a reddish brown spiral band. The last quarter-turn of the body whorl descends gently to the aperture. The peristome is expanded and reflected, most strongly on the basal and inner lips; the inner lip covers approximately  $\frac{1}{3}$  of the umbilicus. Dimensions: diameter (exclusive of expanded lip) 23.4 mm, height 14.0 mm, diameter of umbilicus 2.6 mm; whorls (counted by method of Pilsbry [1939]) 6.75.

The holotype agrees with all later authors' interpretation of *H. diabloensis* but is not precisely matched in any samples we have been able to examine. Its spire is more conical and the body whorl is more tightly coiled than usual in the species. Probably no subsequent collections have been made from the type population. The area around New Idria is extremely barren and affords little of the type of cover that *H. diabloensis* inhabits elsewhere. The vicinity of Panoche Pass (which was probably the route that Brewer took to New Idria) seems a more likely source; but pending additional field work in this sparsely prospected part of the inner Coast Range, the type locality and the southern limit of the species' range must remain open questions.

#### Acknowledgments

We are grateful to Clyde Roper for the discovery of the holotype of *H. diabloensis* and to Paul F. Allen and F. G. Hochberg for the circumstances that made it possible. David R. Lindberg, Terrence M. Gosliner, Robert Van Syoc, and James H. McLean supplied comparative material and information.

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**Density, Distribution, and Feeding of the Marine Snail  
*Norrisia norrisi* (Mollusca: Gastropoda) on the Kelp  
*Macrocystis pyrifera* (Phaeophyta: Laminariales)**

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**Abstract.**—Grazing by the snail *Norrisia norrisi* on *Macrocystis pyrifera* was studied off Santa Catalina Island, California. Snails occurred on all parts of *M. pyrifera* plants and averaged 8.7 individuals/plant. Laboratory feeding experiments indicated that *N. norrisi* consumed significantly more sporophyll tissue (53%) than either mature (23%) or apical (24%) laminae. Snails consumed approximately 1–3% of the estimated daily *M. pyrifera* production. Consequently, grazing by these snails may not be significant under normal conditions. However, the strong preference for sporophyll tissue suggests that *N. norrisi* could have significant effects on the reproductive capacity of *M. pyrifera*, especially in kelp beds damaged by storms or other disturbances.

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Grazing by mobile herbivores may be extremely important in the regulation of local algal species composition and ultimately community structure (e.g., Paine and Vadas 1969; Dayton 1975; Lubchenco and Menge 1978; Lubchenco and Gaines 1981). Herbivorous gastropods, crustaceans, echinoids, and fishes play important roles in the natural loss of tissues in the giant kelp, *Macrocystis pyrifera* (L.) C. Agardh (Leighton 1966, 1971; Leighton et al. 1966).

The trochid snail *Norrisia norrisi* (Sowerby, 1838) is a common and conspicuous herbivore in kelp forests ranging from Point Conception, California to Isla Asunción, Baja California, Mexico (Abbott and Haderlie 1980). This snail is especially common in *M. pyrifera* forests off Santa Catalina Island, California. Leighton (1971) reported *N. norrisi* to be an occasionally serious grazer on *M. pyrifera* and suggested that this snail may be a major biological factor affecting small stands of the kelp.

*Norrisia* is found on all parts of *M. pyrifera* and is known to undergo diurnal vertical migrations along the kelp fronds (Miller 1975; Abbott and Haderlie 1980). Feeding preference for various kelp tissues may account for patterns of distribution and movement in *N. norrisi*. These patterns, however, may be the result of predator avoidance responses or competitive interactions.

This study was designed to: (1) test the hypothesis that tissue preference accounts for the distribution and diurnal migration of snails along kelp fronds; and (2) examine the potential effects of grazing by *N. norrisi* on *M. pyrifera*. The following points are addressed: (1) density and size-distribution of snails at the study site; (2) density and size-distribution of kelp at the study site; and (3) feeding rates and preferences of snails on various kelp tissues.



### Methods

The study site was a *Macrocystis pyrifera* forest located off the northwest end of Bird Rock, Isthmus Cove, Santa Catalina Island, California (35°25.4'N, 180°30.8'W). A 30 m transect was established at the site along a 6–9 m depth contour. Sampling was performed using SCUBA during daylight hours in August 1982.

Population density and size-distribution of *Norrisia norrisi* were estimated along the transect from 15 randomly chosen adult *M. pyrifera* plants. Plants were considered adults if they formed a canopy layer. Frond counts were recorded for all plants sampled. All snails occurring on the plants were collected and taken to the Catalina Marine Science Center (CMSC) for analysis. Snails were counted, and the maximum shell diameter measured to the nearest 0.1 mm using calipers. The density and sizes of *M. pyrifera* plants were estimated along the transect from 10 randomly chosen 5.0 m<sup>2</sup> quadrats. All adult plants with holdfasts occurring within the quadrats were counted, and number of fronds per plant recorded.

Twenty-one snails collected during the population census were selected for use in tissue preference and feeding rate experiments. These snails were healthy (active under laboratory conditions) and ranged between 30.0 and 40.0 mm in shell diameter. All experimental individuals were maintained in running sea water aquaria and provided with food (*M. pyrifera* laminae and sporophylls) until tested. Tests were performed within one week of collection. A feeding experiment consisted of snails being provided with approximately equal quantities of sporophyll tissue, mature laminae, and apical laminae. Seven replicates of three snails each were tested over two 24-hour feeding periods. Three controls (kelp tissues with no snails) per feeding period permitted correction for any weight change of kelp due to deterioration or growth. Consumption, corrected for weight changes in the controls, was measured as the difference in blotted wet weight of kelp tissues before and after each feeding period. This method has been shown to be a valid way to measure algal consumption by marine herbivores (e.g., Leighton 1966). Weight changes in the controls were negligible, averaging less than 2% of that in the experimental containers.

### Results

*Norrisia norrisi* occurred on all parts of the *Macrocystis pyrifera* plants. However, snails appeared concentrated in the canopy and sporophyll bundles. Although not quantified, there did not appear to be a significant difference in the number of snails collected from sporophyll bundles vs. the canopy. There appeared to be fewer snails on lower parts of the plants during morning dives than afternoon dives, suggesting that snails migrated downwards during the day and upwards at night, in agreement with the migration pattern previously noted by Miller (1975).

The mean number of *N. norrisi* per *M. pyrifera* plant was 8.7 individuals (SD = 5.4; N = 15) and mean shell diameter was 36.1 mm (SD = 6.4; N = 131). More than 60% of the snail population was in the 30.0–40.0 mm size-classes (Fig. 1). No juvenile snails (<15 mm) were observed during the study. The density of *M. pyrifera* plants measured at the study site averaged 1.7 individuals per 5.0 m<sup>2</sup> (SD = 1.4; N = 10) (=0.34/m<sup>2</sup>). Plants in the 5.0 m<sup>2</sup> quadrats averaged 23.2 fronds per plant (SD = 11.7; N = 17), whereas plants sampled for snails averaged



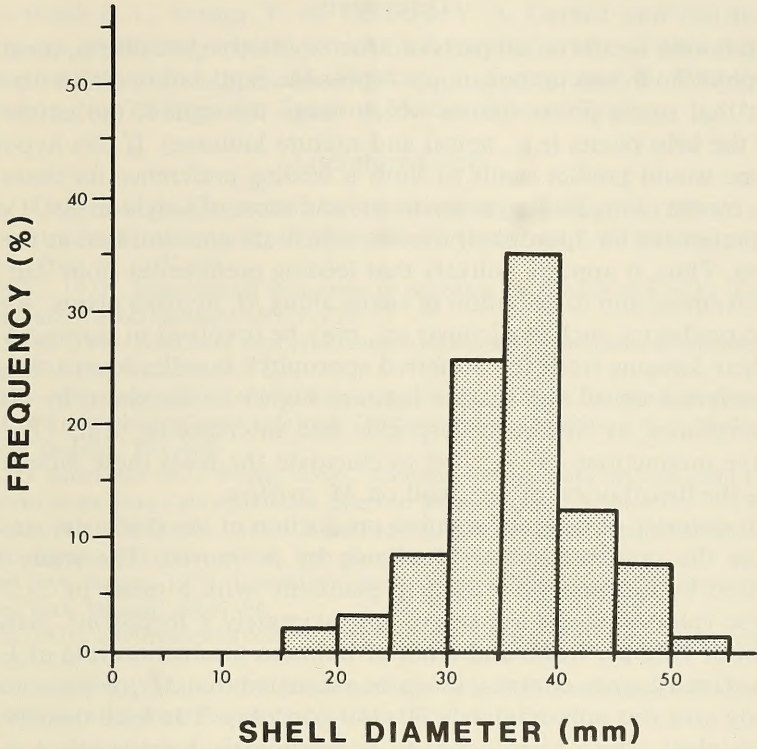


Fig. 1. Size-frequency distribution of *Norrisia norrisi* on *Macrocystis pyrifera* at study site during August 1982: Santa Catalina Island, California. Data are maximum shell diameter in mm.  $\bar{X}$  = 36.1; SD = 6.4; N = 131.

28.1 fronds per plant (SD = 11.4; N = 15). These two values (fronds/plant) are not significantly different ( $P > .05$ , Kolmogorov-Smirnov test). Plants sampled for snails were therefore assumed representative of the adult kelp population.

Results of the feeding experiments (Table 1) indicated a significant difference in consumption of the three tissue types ( $P < .05$ ,  $\chi^2$ -test). Sporophylls were significantly preferred over either mature laminae or apical laminae ( $P < .05$ , Duncan's multiple range test). There was no significant difference in preference between mature and apical laminae. *Norrisia norrisi* consumed an average of 0.65 g wet weight kelp/snail/day.

Table 1. Results of laboratory tissue preference and feeding rate experiments of *Norrisia norrisi* on *Macrocystis pyrifera*. Experiments consisted of 20 replicates: 14 experimentals with 3 snails each and 6 controls with no snails (see text for details). Data are blotted wet weight of kelp tissues.

|                            | Sporophyll<br>tissue | Mature<br>laminae | Apical<br>laminae | Total |
|----------------------------|----------------------|-------------------|-------------------|-------|
| Total consumption (g)      | 14.4                 | 6.1               | 6.6               | 27.1  |
| % consumption              | 53                   | 23                | 24                | 100   |
| Feeding rate (g/snail/day) | 0.34                 | 0.15              | 0.16              | 0.65  |



### Discussion

*Norrisia norrisi* occurs on all parts of *Macrocystis pyrifera* plants, ranging from the sporophylls to fronds to the canopy. A possible explanation of this distribution pattern is that snails prefer tissues which range throughout the entire vertical height of the kelp plants (e.g., apical and mature laminae). If this hypothesis is correct, one would predict snails to show a feeding preference for these tissues. However, results of my feeding experiments and those of Leighton (1971) indicate a strong preference for sporophyll tissues, which are concentrated at the base of kelp plants. Thus, it appears unlikely that feeding preferences alone can account for the movement and distribution of snails along *M. pyrifera* plants. Avoidance of benthic predators, such as *Octopus* sp., may be involved in causing *N. norrisi* to shift their foraging from the preferred sporophyll bundles low in the plant to the less preferred apical and mature laminae higher in the plant. Investigations of such predators, as well as intraspecific and interspecific (e.g., *Tegula* spp.) competitive interactions, are needed to elucidate the roles these factors play in regulating the distribution of this snail on *M. pyrifera*.

A rough estimate of daily *M. pyrifera* production at the study site was needed to examine the potential effects of grazing by *N. norrisi*. The study site was characterized by a density of 0.34 kelp plants/m<sup>2</sup> with a mean of 23.2 fronds/plant; these values indicate a mean of approximately 8 fronds/m<sup>2</sup>. Assuming a wet weight of 1 kg per frond and a net or biomass production rate of 1–3% per day (V. A. Gerard, pers. comm.), it can be estimated that *M. pyrifera* production at the study area was approximately 80–240 g/m<sup>2</sup>/day. The snail density was 8.7 individuals/plant, which corresponds to approximately 3 snails/m<sup>2</sup>. At a feeding rate of 0.65 g kelp/day these snails were consuming 1.95 g kelp/m<sup>2</sup>/day. Thus, *N. norrisi* appeared to consume roughly 1–3% of the daily kelp production (or 0.025% of standing crop/day) at the study site.

*Norrisia norrisi* probably has little effect on healthy stands of *M. pyrifera* at these low feeding rates. However, if conditions were to change such that densities increased to an average of 30 or more snails per plant (e.g., after loss of plants due to storms or anomalous sea temperatures), a feeding rate of 10% or more daily production may be realized. Such a feeding rate, in combination with grazing pressures by other herbivores (e.g., snails, crabs, fishes), may have serious effects on populations of *M. pyrifera*. For example, V. A. Gerard (pers. comm.) has noted *N. norrisi* causing visible damage to *M. pyrifera* at Corona del Mar, California during July–August 1981, after most of the plants had disappeared following storms. In this instance, the kelp forest was reduced to a low density, the plants were relatively small, and there were snails grazing all over them. Furthermore, the strong preference for sporophylls suggests that *N. norrisi* may have significant effects on reproductive capabilities of *M. pyrifera*. These effects may be especially pronounced in kelp beds damaged by storms, unusually high sea temperatures associated with events such as the 1983–1984 El Niño, and other disturbances.

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## Catastrophic Flooding and Distributional Patterns of Pacific Cordgrass (*Spartina foliosa* Trin.)

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**Abstract.** — The distribution of Pacific cordgrass (*Spartina foliosa* Trin.) is patchy within the southern California region, within particular wetlands and within clones. Small-scale patchiness cannot be fully explained by environmental variables. However, study of cordgrass before and after catastrophic flooding has led to an alternative model. It is proposed that establishment is most likely after fresh water dilutes soil salinities and that expansion and persistence depend on previous densities, disturbances, and competitors. The lower intertidal marsh soils are nearly always hypersaline (35–45 ppt), and germination of cordgrass seed is rare. Reproduction is primarily by rhizomes and tillers. Soil salinity is reduced with episodic flooding, at which time cordgrass can establish seedlings and invade suitable habitats. Clones spread more rapidly after flooding. Within clones, densities increase after flooding in proportion to their pre-flood densities. Cordgrass is establishment limited, and historical events exert substantial control over its distribution and abundance.

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Pacific cordgrass (*Spartina foliosa* Trin.) dominates the lower marsh habitats of certain Pacific coastal wetlands from Baja California north to Humboldt Bay (Macdonald and Barbour 1974). The absence of cordgrass from many coastal salt marshes has not been explained; yet the question of what controls its range is important because management agencies (cf. Light-footed Clapper Rail Recovery Team 1977) recommend expanding its distribution in order to enhance habitat for the endangered light-footed clapper rail (*Rallus longirostris levipes*). While planting techniques have been developed for wetland restoration purposes (Zedler 1984), the range of conditions essential for cordgrass growth need to be determined.

Compared to the smooth cordgrass (*Spartina alterniflora* Loisel.), which dominates salt marshes throughout the Atlantic Coastal region, the distribution of the Pacific species is highly patchy. In southern California, it occurs in only 7 of 26 coastal wetlands (Fig. 1). Within those 7 wetlands, it is limited to a relatively narrow range of elevations (approx. 2–7 dm above Mean Sea Level [MSL] or 3.5–5.2 ft above Mean Lower Low Water [MLLW], based on Zedler 1977), but it fails to occupy all sites within that intertidal range. Several large areas of seemingly suitable habitat lack the species or have only small patches of cordgrass. Finally, within clones of cordgrass, densities are quite variable.

In 1979, a detailed study of the lower salt marsh was begun at Tijuana Estuary, focusing on environmental variables that were known to influence the Atlantic Coast species (elevation, salinity, soil aeration; cf. review by Chalmers 1982).

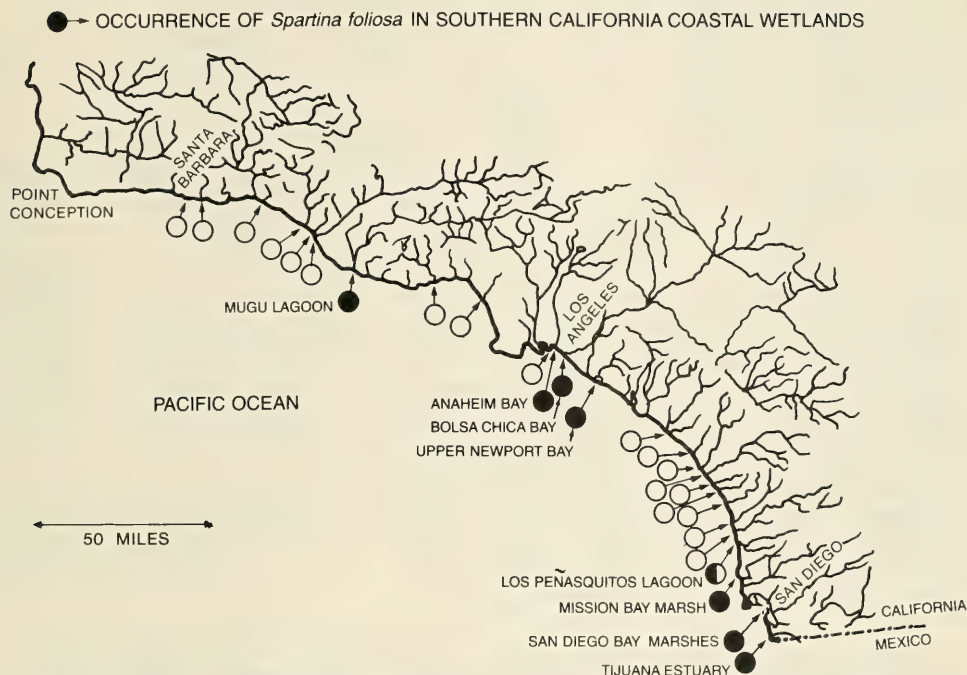


Fig. 1. Cordgrass occurs in only 7 of southern California's 26 coastal wetlands (darkened circles). Sometime after 1939, it disappeared from Los Peñasquitos Lagoon (half-darkened circle).

However, the factors measured at Tijuana Estuary explained little of the variability in the cordgrass data (J. Zedler unpublished data), and results were put aside. After the catastrophic floods of 1980, cordgrass distribution expanded within the Tijuana Estuary, and a monitoring program (1979–present) documented significant increases in cordgrass growth. The post-flood responses of the species suggested new cause-effect hypotheses. This paper summarizes a variety of observations and field experiments that help to explain patchiness of cordgrass within clones, within the intertidal zone, and within the region.

## Methods

### *Monitoring the Cordgrass Marsh*

In March 1979, 8 transects were established in the cordgrass-dominated low marsh at Tijuana Estuary (32°34'N, 117°7'W). Each transect began at a random point on the adjacent channel edge and proceeded landward to a point just beyond the 1979 upper limit of cordgrass. Sampling stations were permanently staked at 5-meter intervals, with 9–20 stations per transect and a total of 101 stations. Each September, cordgrass stems were counted and heights were measured in 0.25 m<sup>2</sup> circular quadrats at all stations. Cover of other species (not readily counted) was estimated by cover class (Kershaw 1973).

Several environmental factors were assessed at the onset of monitoring, and at intervals thereafter. Interstitial salinities were measured by expressing a drop of soil water onto an A-O Salinity Refractometer. Because root biomass is highest between 0–20 cm, the soil water sample was taken from approximately 10 cm



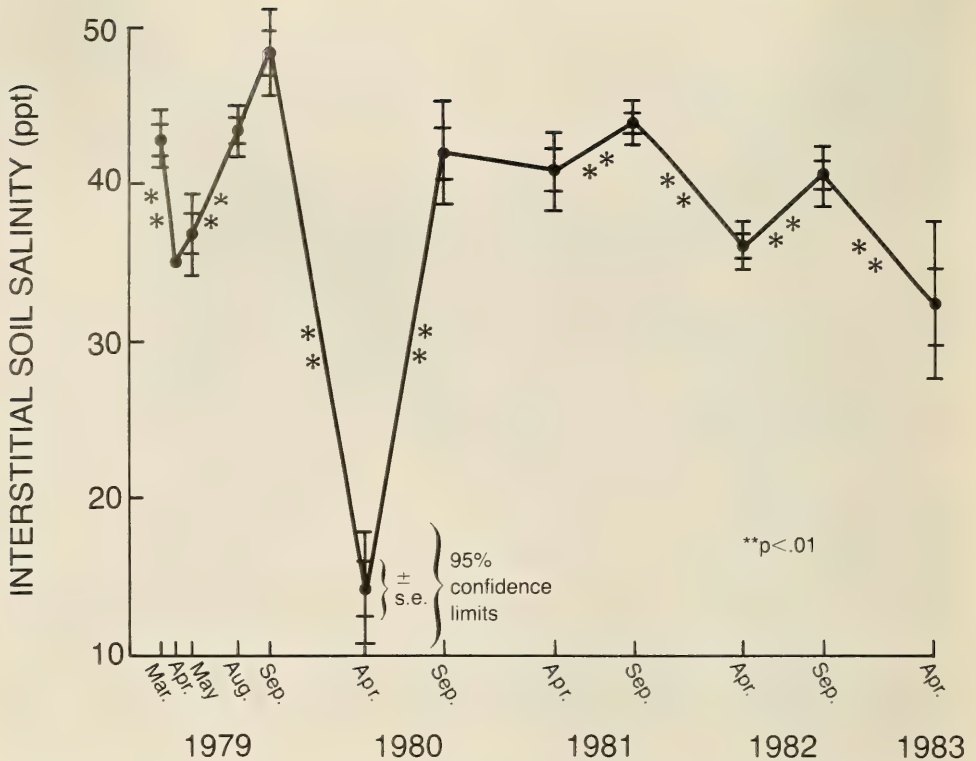


Fig. 2. Catastrophic flooding in January and February 1980 lowered the salinity of cordgrass soils. Brackish conditions have not recurred since the "hundred-year" flood. Data for this transect (TJE-31,  $n = 13$  stations) provide the longest record of soil salinity.

depth. Soil salinity measurements began in March 1979 at Transect TJE-31 (Fig. 2). The salinity minimum occurred in April and the maximum in September. Beginning in fall 1979, all transects were monitored in April and September of each year.

In September 1979, the elevation of each quadrat was measured, using a Wild Automatic Level referenced to Army Corps of Engineers benchmarks. At the same time, soil samples were collected in 250-ml cans to obtain soil moisture (loss on drying), bulk density (weight of dry soil/volume), and soil organic matter (loss on ignition at 500°C in a muffle furnace). Soil oxygen content was assessed in buried test tubes (after Boggie 1977). Plastic tubes (45 ml, perforated and lined with Teflon) were filled with a 35 ppt solution of Instant Ocean, stoppered, and buried in the top 10 cm of soil at each sampling station. One week later, the oxygen content of the solution was measured in situ with a YSI oxygen electrode. Soil temperature was read from the YSI thermister in the above solution.

#### Competition Experiments

The possible influence of competitive interactions was suggested by a negative relationship between cordgrass and cover of other species. A field experiment was designed to test the hypothesis that the succulent vegetation (primarily *Salicornia virginica* L. with some *Batis maritima* L.) reduced cordgrass density and biomass.

Table 1. Cordgrass variability within the lower marsh at Tijuana Estuary. Data are from September 1979; n = 90 quadrats with cordgrass present.

|                                            | Mean | S.E.  | Range |
|--------------------------------------------|------|-------|-------|
| Density (#/0.25 m <sup>2</sup> )           | 13.7 | (1.3) | 1-59  |
| Average height in quadrat (cm)             | 68.7 | (1.3) | 21-94 |
| Total stem length (meters/m <sup>2</sup> ) | 37.7 | (3.6) | 2-150 |

In February 1981, three areas with both cordgrass and succulents were chosen between transects TJE-30 and TJE-33. Four 1 m<sup>2</sup> plots were delimited at each area and randomly assigned to treatments. One served as a control; cordgrass was removed (clipped to ground level) from a second; succulents were removed from a third; and all above-ground biomass was removed from a fourth to determine initial biomass. At three times during the growing season, the removal plots were cleared of resprouting individuals by clipping to ground level. The resprouts were oven dried to determine the cumulative biomass that had to be cleared. All above-ground biomass was harvested in October 1981 and dried to constant weight at 80°C.

#### *Studies within the Intertidal Zone*

Elsewhere in Tijuana Estuary, patches of cordgrass occurred in succulent-dominated vegetation along the edge of two abandoned sewage lagoons. These patches were marked and their north-south and east-west diameters measured in March and October of 1979 and again in July 1980. Patches that became established after the floods were marked and measured in July 1980. The area of each patch was estimated as an ellipse, and changes in diameter and area were summarized for pre- and post-flood years.

#### *Regional Distribution*

Historical records of cordgrass in southern California coastal wetlands were examined (Purer 1942, California Fish and Game Coastal Wetlands Series Reports 1970-76, and Macdonald and Barbour 1974) for comparison with recent observations (Zedler 1982). One major change has occurred; the luxuriant stands noted at Los Pensaquitos Lagoon in 1939 (Purer 1942) are no longer present. An attempt was made to reestablish cordgrass at Pensaquitos Lagoon by planting 40 sprigs

Table 2. Habitat conditions within the lower marsh at Tijuana Estuary. The data are from August-September 1979 and include 101 sampling stations, 90 of which had cordgrass present.

|                            | Mean    | S.E.   |
|----------------------------|---------|--------|
| Elevation, MSL             | 67 cm   | (0.9)  |
| Interstitial soil salinity | 44 ppt  | (0.8)  |
| Soil moisture              | 250%    | (9.8)  |
| Soil organic matter g/g    | 20%     | (0.7)  |
| and mg/cc                  | 57      | (1.1)  |
| Bulk density mg/cc         | 327     | (13.0) |
| Soil oxygen                | 0.7 ppm | (0.04) |
| Soil temperature           | 21°C    | (0.4)  |



Table 3. Correlation coefficients ( $r$ ) between cordgrass and environmental variables. Non-significant ( $P > 0.05$ ) coefficients are not listed.

| Average height | Density | Total stem length | Environmental variable               |
|----------------|---------|-------------------|--------------------------------------|
|                | -0.3    | -0.3              | Elevation                            |
|                | -0.2    | -0.3              | % Organic matter (g/g)               |
|                | -0.3    | -0.3              | Organic matter (mg/cc)               |
|                | -0.2    |                   | Cover of <i>Salicornia virginica</i> |
|                | -0.2    | -0.2              | Cover of <i>Batis maritima</i>       |
| -0.3           | -0.3    | -0.3              | Cover of misc. species               |

within the low-marsh succulent canopy in February 1980. Survivorship was assessed monthly.

## Results and Discussion

### *Patterns of Cordgrass Density and Height*

Cordgrass was present at 90 of the 101 sampling stations at Tijuana Estuary in 1979, but both densities and heights were highly variable (Table 1). Densities within the 0.25 m<sup>2</sup> quadrats had a variance-to-mean ratio of 11, indicating considerable patchiness. On the average, there were 13.7 stems/quadrat, or 55/m<sup>2</sup>. Heights were averaged by quadrat, then for the 90 stations (mean = 68 cm). Total stem length, a non-destructive measure of biomass, averaged nearly 38 m per square meter. Data on cordgrass habitat (Table 2) were also variable, but intertidal elevation was usually low, and soils were generally hypersaline, moist, organic, warm, and nearly anaerobic in fall.

Interrelationships between cordgrass and its habitat were explored by correlating each of the three measures of cordgrass growth (density, average height, and total stem length) with the eight physical variables (cf. Table 2) and the cover data for five taxa (*Salicornia virginica*, *Batis maritima*, *Jaumea carnosa*, *Salicornia bigelovii*, and miscellaneous [not separated]). Of the 39 resulting correlations ( $3 \times 13 = 39$ ), 12 were significant at the 5% level (Table 3), but none of the  $r$  values exceeded 0.3. Three types of habitat factors were indicated—elevation, soil organic matter (both as fraction of soil weight and of soil volume) and other species (*Salicornia virginica*, *Batis maritima*, and miscellaneous). The negative correlation with elevation reinforced the obvious pattern of a landward decline in cordgrass abundance. The negative relationship between cordgrass and organic matter was not expected, since roots were included in soil samples. The negative relationship between cordgrass and other species suggested competition between these groups, and experiments to test for interspecific effects were later set up (cf. Methods).

An additional attempt to explain the variability in cordgrass utilized a step-wise linear multiple regression analysis (BMD Statistical Package, Univ. of Calif., Los Angeles). Separate analyses were performed for each of the three dependent variables (density, average height, and total stem length), but it was never possible to explain more than 29 percent of the variability in cordgrass data (Table 4). The significant ( $P < 0.05$ ) independent variables indicated by these analyses were cover of other species, soil organic matter, and soil temperature. Overall, this exercise did little to improve our understanding of growth-limiting factors, and

Table 4. Summary of step-wise linear multiple regression analyses for three cordgrass variables ( $n = 101$  stations, 90 of which had cordgrass present). In each analysis, the significant ( $P < 0.05$ ) variables are listed with their contribution to the reduction of the regression sums of squares.

|                                                                          | Cumulative<br>SS reduced |
|--------------------------------------------------------------------------|--------------------------|
| 1. Dependent variable = density in 0.25 m <sup>2</sup> circular quadrats |                          |
| Independent variables = cover of misc. species (not separated)           | 0.10                     |
| percent soil organic matter (g/g)                                        | 0.15                     |
| soil temperature                                                         | 0.20                     |
| soil organic matter (mg/cc)                                              | 0.29                     |
| 2. Dependent variable = average height                                   |                          |
| Independent variables = cover of misc. species (not separated)           | 0.08                     |
| cover of <i>Salicornia virginica</i>                                     | 0.14                     |
| 3. Dependent variable = cordgrass total stem length (m/m <sup>2</sup> )  |                          |
| Independent variables = organic matter (mg/cc)                           | 0.11                     |
| cover of misc. species (not separated)                                   | 0.18                     |
| cover of <i>Batis maritima</i>                                           | 0.24                     |
| soil temperature                                                         | 0.28                     |

a satisfactory explanation of cordgrass distributions did not emerge. The environmental variables that were measured were not controlling cordgrass distribution.

### *The Influence of Competitors*

Purer (1942) suggested that competition was important in limiting the landward distribution of salt marsh species, because she could not identify an environmental stress that would preclude growth at higher elevations. Mahall and Park (1976) expressed an alternative view, that physical factors were responsible for the upper boundary of cordgrass at two San Francisco Bay sites. Their suggestion was based on an ecotone where cordgrass and pickleweed overlapped relatively little and environmental conditions appeared poor for both species. In the Tijuana Estuary data set, cordgrass and pickleweed co-occurred in approximately 90% of the quadrats, with a negative correlation between the two species. Hence, field competition experiments were developed.

Field experiments showed that removal of other species increased cordgrass density 2.3 times, while control plots decreased in cordgrass density during the 1981 growing season (Table 5). Correspondingly, biomass of cordgrass increased 7.4 times in the removal plots and only 4.3 times in control plots between February and October 1981. These results suggest competitive effects, but they do not identify limiting factors. Cordgrass (a  $C_4$  species) may be favored by greater light availability following removal of associated species (mostly  $C_3$ ). However, it is the tallest marsh plant, and it seems unlikely that light is the main factor for which it competes. More recently, nitrogen limitation has been identified by Covin (1984) using combined fertilization and removal experiments at Tijuana Estuary.

The 1981 removal experiment verified two of the multiple regression findings—that other species reduce the density and biomass of cordgrass, and that other species explain only part of the variation in cordgrass biomass. The fact that



Table 5. The effect of removing succulents (primarily pickleweed) from plots with cordgrass ( $n = 3 \text{ } 1 \text{ m}^2$  plots/treatment). The biomass of succulents removed on Feb. 27 averaged  $1085 \text{ g/m}^2$  (S.E. = 166). The biomass of harvested resprouts totalled  $216 \text{ g/m}^2$ . The Feb. 27 biomass of cordgrass was determined from 3 quadrats where all vegetation was removed.

|                                              | Feb. 27   | July 6    | Oct. 5           |        |
|----------------------------------------------|-----------|-----------|------------------|--------|
|                                              | $\bar{x}$ | $\bar{x}$ | $\bar{x}$        | S.E.   |
| Density of cordgrass (number/ $\text{m}^2$ ) |           |           |                  |        |
| With succulents (control)                    | 65        | 31        | 53               | (6.2)  |
| Without succulents                           | 65        | 81        | 152 <sup>1</sup> | (2.5)  |
| Biomass of cordgrass ( $\text{g/m}^2$ )      |           |           |                  |        |
| With succulents (control)                    | 56        |           | 240              | (9.5)  |
| Without succulents                           | 56        |           | 417 <sup>2</sup> | (95.0) |

<sup>1</sup> Significantly different from control, t-test,  $P < 0.01$ .

<sup>2</sup> Significantly different from control, t-test,  $P < 0.05$ .

removing competitors did not lead to maximum biomass of cordgrass (over  $1000 \text{ g/m}^2$  in pure stands; Zedler et al. 1980) suggests that other factors are also important. Because cordgrass usually reproduces vegetatively by rhizomes and tillers, it may take more than a year for a clone to take full advantage of reduced competition. However, the analysis of cordgrass populations after the unusual events of 1980 suggested that growth can increase greatly within a single growing season and that variations in cordgrass are better explained by pre-flood densities than by environmental factors.

#### *The Role of Catastrophic Flooding*

Repeated heavy rainfall led to flooding in January and February of 1980 (Zedler 1983), and the hypersaline marsh soils became brackish for a short time thereafter (Fig. 2). By September 1980, there were substantial increases in cordgrass density (24%), height (23%), and total stem length (39%) for the combined data set (101 stations; Fig. 3).

The changes were not uniform across the marsh. Among the eight transects, cordgrass density increased in five, decreased in one, and remained similar in two (Table 6). The density responses were not correlated with pre- or post-flood environmental conditions. However, densities after flooding were related to pre-flood densities in some locations. For five of the eight transects, the 1980 densities were significantly correlated with 1979 densities, accounting for up to 85% of the 1980 variability (Table 6). The remaining transects had evidence of patchy mortality due to flood-deposited debris (including piles of stakes used in upstream tomato fields); those 1980 densities were not related to the respective 1979 values. These patterns were investigated at a smaller scale by analyzing quadrats that increased separately from quadrats that decreased (ignoring 7 quadrats that did not change). Correlations between 1980 and 1979 densities were expected to be higher if vegetative propagation increased densities and lower if local disturbances caused declines. The results were consistent with that explanation; more of the 1980 variability in density could be accounted for in quadrats that increased ( $n = 68$ ;  $r^2 = 0.67$ ) than in quadrats that decreased ( $n = 26$ ;  $r^2 = 0.44$ ).

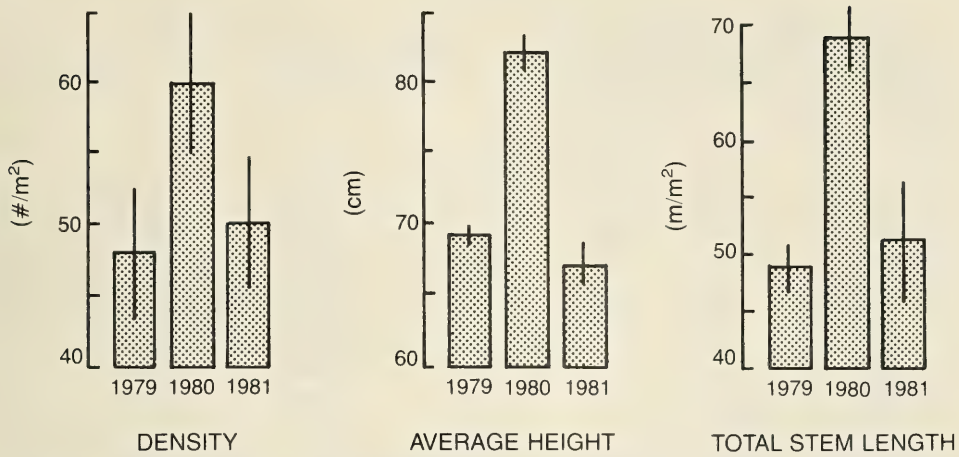


Fig. 3. Cordgrass height, density, and biomass estimates were significantly ( $P < 0.05$ ) different in September of 1979 and 1980 (after flooding). Standard errors about the means (vertical lines) show overlap for 1979 and 1981 indicating rapid return to pre-flood conditions. Height and biomass data are for 90 quadrats with cordgrass present, while density data ( $n = 101$ ) included the 21 quadrats that lacked cordgrass.

#### *Horizontal Patterns of Cordgrass*

The above data came from an extensive cordgrass stand with relatively little human disturbance. However, two abandoned sewage lagoons at Tijuana Estuary had only isolated cordgrass patches among the pickleweed marsh. Observations before and after the 1980 flood showed that catastrophic events influence establishment and spread of cordgrass. Censuses during 1979 documented 33 patches of cordgrass around the old sewage lagoons (Fig. 4). Measurements of the diameters of 15 patches both early and late in the growing season gave expansion rates of 1.1 m/yr before the floods. A recensus in July 1980 located 103 patches, and a remeasurement of the 15 patches gave significantly ( $P < 0.05$ ) higher diameter expansion rates of 2.4 m/yr for the post-flood growing season. Clearly, patches established and spread significantly more after flooding than before. These data are consistent with laboratory studies of cordgrass seed germination (Seneca 1974, Zedler 1984). Fresh water stimulates germination and early seedling growth. Reduced soil salinities and related flood effects (e.g., added nutrients) increase cordgrass growth and patch size.

Since 1980, it has become increasingly difficult to follow expansion because patches have begun to merge (Fig. 4). The process of establishment, expansion, and merger may well represent the way in which continuous stands of cordgrass have developed. The cordgrass marsh in the main arm of Tijuana Estuary could include several genetically distinct clones that established after various disturbance events and later emerged.

#### *Regional Occurrence*

At the regional level, cordgrass occurs primarily in coastal wetlands with a long history of good tidal flushing (Fig. 1). Eilers (1980) found a small patch of cordgrass in a portion of Bolsa Chica that had lacked tidal flow for 80 years. However the



Table 6. Summary of cordgrass densities ( $n = 101$ ,  $0.25 \text{ m}^2$  quadrats) at Tijuana Estuary before (1979) and after (1980) major flooding. Means were compared using Kruskal-Wallis ANOVA and Newman-Keuls multiple range tests, and year-to-year product-moment correlation coefficients were calculated.

| Transect | # Quads. | Number/ $0.25 \text{ m}^2$ |      | Change   | Year-year correlation       |
|----------|----------|----------------------------|------|----------|-----------------------------|
|          |          | 1979                       | 1980 |          |                             |
| TJE-2    | 9        | 24.7                       | 25.7 | n.s.     | $r = .36$ n.s. <sup>1</sup> |
| TJE-5    | 9        | 10.8                       | 14.0 | increase | $r = .88^{**}$              |
| TJE-28   | 10       | 23.1                       | 12.3 | decrease | $r = .02$ n.s. <sup>2</sup> |
| TJE-30   | 11       | 11.5                       | 17.5 | increase | $r = .93^{**}$              |
| TJE-31   | 13       | 10.6                       | 14.2 | increase | $r = .33$ n.s. <sup>3</sup> |
| TJE-33   | 20       | 9.3                        | 15.2 | increase | $r = .75^{**}$              |
| TJE-34   | 16       | 9.7                        | 15.8 | increase | $r = .61^*$                 |
| TJE-37   | 13       | 5.7                        | 9.6  | n.s.     | $r = .89^{**}$              |

<sup>1</sup> The mean is similar but only 1 quadrat did not change in density—3 decreased and 5 decreased.

<sup>2</sup> This transect had areas of mass mortality (cause unknown).

<sup>3</sup> Two rather dense quadrats were smothered by debris in 1980. Omitting them from the correlations gives  $r = .83^{**}$ .  $*$  =  $p < 0.05$ .  $^{**}$  =  $p < 0.01$ .

site was in a channel just behind a dune, where tidal water may have seeped through the sand. His year-long data on soil moisture (mean = 78% of soil wet weight) and soil salinity (mean = 35 ppt) indicate seawater influence, if only indirect.

The loss of cordgrass from Los Penasquitos Lagoon may have resulted from periods of lagoon closure when evaporation dried soils and concentrated salts. Carpelan (1969) documented water salinity of 60 ppt in 1959, and the lagoon remained non-tidal until 1966 (Bradshaw 1968). Neither extremely saline nor dry soil favors cordgrass. Rather, it is abundant in areas of frequent tidal wetting with relatively constant (40–45 ppt) salinity.

The 1980 transplants to Los Pensaquitos Lagoon were expected to survive only if good tidal flushing prevailed. Because of heavy rainfall, soil salinities were low that year (34 ppt on the February 12 transplanting date, reduced to 22 ppt by later storms). On 24 March, 27 of the 40 plants were alive, and most mortality was attributable to grazing by small mammals (voles?). In May, a sand bar blocked the ocean connection, and the lagoon was covered with 30–60 cm of brackish water through most of June. Only 2 transplants were alive in July. It appeared that low salinities allowed initial establishment, but that the disturbances associated with lack of tidal flushing (i.e., unusually long inundation and competition from well-established succulents) prevented their persistence.

### *Implications for Other Species*

Does the observation that catastrophic flooding is important to the distribution of cordgrass apply more generally to other halophytes? For species that do not establish readily from seed, we can speculate that unusual events are necessary to allow establishment and/or substantial increases in their spatial distributions. The event may be flooding, disturbances such as wrack deposition (Oliver 1981; J. Hartman, pers. comm.), or unusual weather. The abnormally long rainy season of 1983 triggered germination in many salt marsh species, including some for which seedlings are usually rare. The general model may well apply to populations

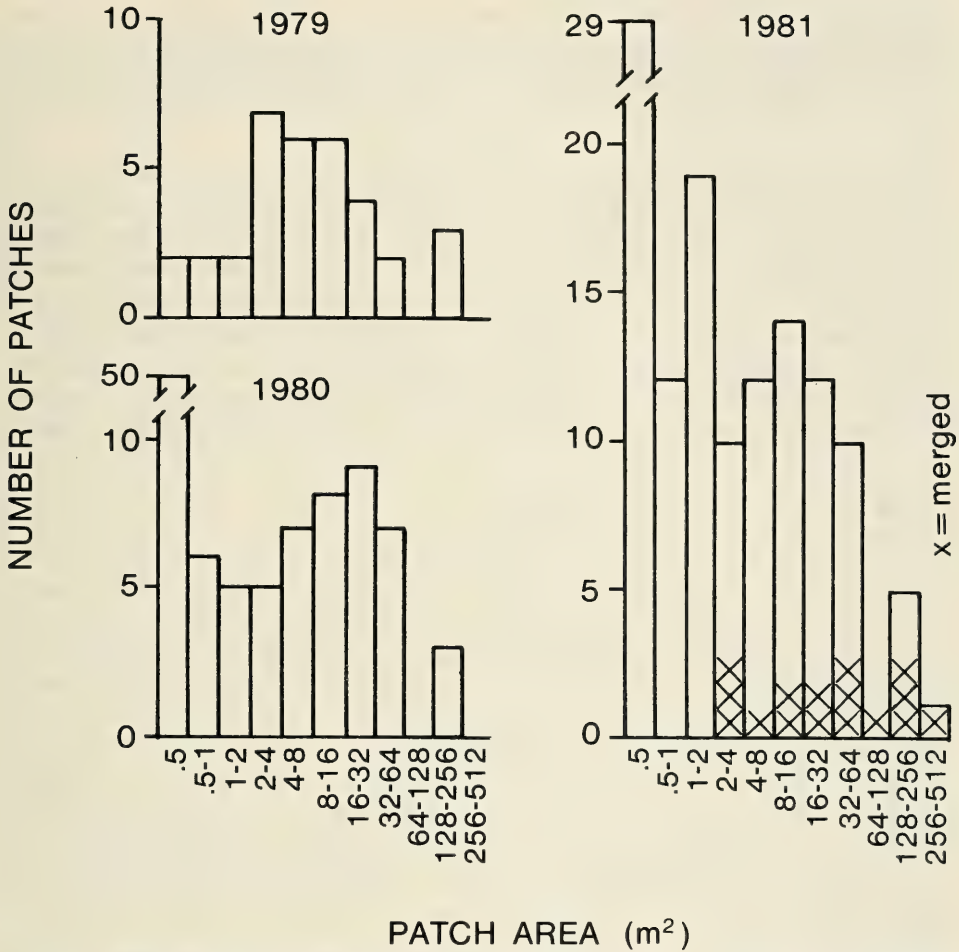


Fig. 4. Both the number of clones and patch sizes for cordgrass near two abandoned sewage lagoons increased following the 1980 flood. In 1979, patches were few and large. In 1980, many new clones appeared, and older patches increased in size. By 1981, many older patches had merged.

of *Limonium californicum*, *Jaumea carnosa*, *Batis maritima*, and *Triglochin cinereum*, which, like cordgrass, are absent from many of the region's coastal wetlands (Zedler 1982). These species have patchy distributions that result in part from vegetative spread, and in part from the rarity of seedling establishment. In contrast, the usual dominant of upper and middle intertidal marshes, *Salicornia virginica*, can and does invade disturbed habitats. Hence, it has a very broad geographic distribution, occurring in saline wetlands of both coastal and inland areas.

#### Summary Model of Cordgrass Distribution

The observations and experimental studies of cordgrass at Tijuana Estuary, during years with and without extreme flooding, have been summarized in a conceptual model of distributional patterns. Whereas previous attempts to explain the occurrence and abundance of cordgrass in southern California have relied



upon characterizations of elevation (Vogl 1966, Zedler 1977) and short-term sampling of soil salinity (cf. Macdonald 1977), the events following catastrophic flooding suggest how extreme events can influence the occurrence and growth of cordgrass. I propose that extreme flooding is important to cordgrass at three spatial scales.

1. At the regional level, well developed stands of cordgrass occur only in coastal wetlands with a long history of good tidal flushing (Fig. 1). We can reconstruct the development of these large stands as a sequence of events that includes flooding. Establishment is most likely when a flood coincides with or follows the arrival of viable seeds. Only then can large numbers of clones become established. Surviving clones expand slowly until floods recur and accelerate vegetative reproduction. Eventually, clones merge and a continuous stand of cordgrass develops. This explanation differs from Macdonald's (1977) model of cordgrass as an early invasion species that is succeeded by succulents after accretion raises the intertidal elevation.

Continual tidal flushing provides habitat that is suitable for cordgrass but sub-optimal for its competitors. Cordgrass can persist in hypersaline conditions if competitors are held below maximum growth. However, if tidal flushing ceases, either on a seasonal basis or for periods of several years, marsh soils become more variable in both salinity and moisture. Under these conditions, succulents such as pickleweed appear to have the advantage, sometimes achieving 2.5 times the productivity rates measured in tidal wetlands (Zedler et al. 1980). Eventually succulents would outcompete any cordgrass clones that might become established.

2. In a local wetland, flooding stimulates expansion of cordgrass horizontally. Cordgrass might invade newly available habitats (e.g., after dikes are breached, sewage lagoons are abandoned, or restoration sites are prepared). But it will establish slowly under average environmental conditions, even if propagules are present. Thus, in restoration projects, transplantation is necessary to insure establishment, and irrigation is recommended to attain maximum growth and survival (Zedler 1984).

Vertically, cordgrass is limited to intertidal elevations below MHHW (7 dm MSL or 5.5 ft MLLW). Flooding is probably not important in controlling this pattern of occurrence. Removal of pickleweed and other succulents within the upper part of the cordgrass range allowed substantial increases in density and biomass. The combined stresses of high soil salinity and low soil moisture at higher elevations probably tip the competitive balance in favor of succulents.

3. Finally, flooding has an important effect within cordgrass clones. Both density and height increased after the 1980 flood, summing to a 39% increase in total stem length. Densities increased in proportion to pre-flood levels, which makes sense for a species that reproduces primarily by tillers and rhizomes. Because of the influence that one year's density has on the next, and the patchy effects of previous disturbances, present-day environmental conditions explain only a fraction of the small-scale pattern.

In order to verify this model of distributional patterns, we need rigorous tests of the response of cordgrass and its competitors to flooding and reduced tidal flooding. While flooding experiments would be hard to implement, smaller scale experiments of salinity reduction have been initiated at Tijuana Estuary (Calif. Sea Grant Project #R/NP-1-13B). In addition, observations of cordgrass mortality

and pickleweed expansion have begun in two salt marshes where tidal flushing has recently ceased. Data sets are incomplete at this writing, but the initial results fail to reject the model. Extreme events appear to have major and lasting effects on southern California's cordgrass marshes.

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## **Deep-Water Biological Assemblages of a Hard-Bottom Bank-Ridge Complex of the Southern California Continental Borderland**

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*Abstract.* — A manned submersible survey of Tanner and Cortes Banks and Santa Rosa-Cortes Ridge, offshore of southern California, U.S.A., was conducted to characterize the hard-bottom, biological assemblages from 14 m to approximately 150 m depth. Four major assemblages were observed; their dominant taxa were: 1) *Eisenia arborea*/erect coralline algae from at least 14 to 40 m; 2) *Agarum fimbriatum*/*Laminaria farlowii* from 40 to 60 m; 3) encrusting coralline algae from 60 to 90 m; and 4) *Florometra serratissima*/ophiuroid from 90 to at least 150 m depth. Subdominate organisms in the shallow assemblage consisted of understory algae (reds and browns) and brittle stars; coralline algae, brown algae, gorgonians and seastars at mid-depth; and seastars, gorgonians and sponges at greater depths. The species and assemblages observed on the banks and ridge are very similar with those occurring in other hard-bottom areas adjacent to the southern California mainland and Channel Islands. However, the depth ranges for these assemblages and several of their species are much greater than observed elsewhere. An exception to this observation is the *Florometra*/ophiuroid assemblage, which is quite common in some deeper-water (100 m to at least 300 m) areas of the Southern California Bight and the Santa Maria Basin. The increased depth ranges and high abundance of the bank assemblages appear to be influenced by water clarity, probably related to their isolation from coastal influences including runoff, the potential for a deep mixed layer caused by strong wave and surge activity, and the greater survey area compared with other studies.

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The subtidal continental borderland along southern California contains extensive areas of hard-bottom habitats including banks, canyons, ridges, and islands (Shepard 1963). Most of the studies (e.g., Pequegnat 1964; Given and Lees 1967;



Neushul et al. 1967; Rosenthal et al. 1974; Turner et al. 1968; Lewbel et al. 1981) on hard-bottom communities in this region were conducted using SCUBA. However, due to limitations caused by decompression requirements, survey depths generally did not exceed 30 m. Community descriptions from deeper rocky habitats (>30 m) are therefore scarce; most information is limited to taxonomic collections acquired by remote sampling techniques.

In recent years the need to characterize hard-bottom communities in deeper water has increased as a result of greater interest in oil and gas development which may directly or indirectly affect these communities. In areas of relatively low relief, studies of deep-water communities can be accomplished using remote sampling methods such as towed cameras, dredges, and trawls. Where the relief is high (e.g., canyons or rocky pinnacles), such methods are usually ineffective due to fouling (Lissner 1979). However, manned submersibles and remotely controlled vehicles have been used successfully to study communities in deep-water areas of high relief (Nekton, Inc. 1981; Dames and Moore 1982; SAIC, 1986).

Tanner and Cortes Banks and Santa Rosa-Cortes Ridge comprise a broad area of rocky shoals and outcrops of high relief located approximately 150 km southwest of Los Angeles, California. Shallow-water communities on the banks were described by Lewbel et al. (1981) and Ecomar, Inc. (1978). Dense stands of southern sea palm *Eisenia arborea* dominated areas shallower than 25 m in depth while coralline algae (encrusting and erect) dominated below 30 m. Fauchald and Jones (1978) and Mearns et al. (1978) studied deeper-water (to 275 m) sand-substrate communities of the banks; however, the deep-water (>30 m) hard-bottom communities are little known.

To gain knowledge of the deeper benthic communities inhabiting rocky areas of Tanner and Cortes Banks and the Santa Rosa-Cortes Ridge, the Bureau of Land Management (now the Minerals Management Service) contracted Interstate Electronics Corporation (IEC) to perform a manned submersible survey from September to November 1978. The goal of this study was to determine the diversity and abundance of the deeper water (30 to 150 m) organisms on the banks and ridge. In this paper, the results of this survey are presented and a comparison is made between assemblages found on the banks and other hard-bottom communities of the Southern California Bight.

### Study Area

Tanner and Cortes Banks and the Santa Rosa-Cortes Ridge are located near the western edge of the Southern California Borderland (Fig. 1). Water depths over the banks range from 4 m to approximately 110 to 160 m near the shelf break; the entire bank-ridge complex rises approximately 2000 m above the surrounding basins (Greene et al. 1975). Topographic highs on the banks are comprised primarily of basalt with intermediate areas of undifferentiated sedimentary and igneous rock (Vedder et al. 1974). The lower slopes, greater than 110 to 160 m in depth, are overlain by sediment layers 6 to 15 m thick; thinner accumulations of sediment (1 to 2 m thick) occur in some shallower areas at the tops of the banks (Vedder et al. 1974).

Compared to the banks, the topographic relief is lower along the Santa Rosa-

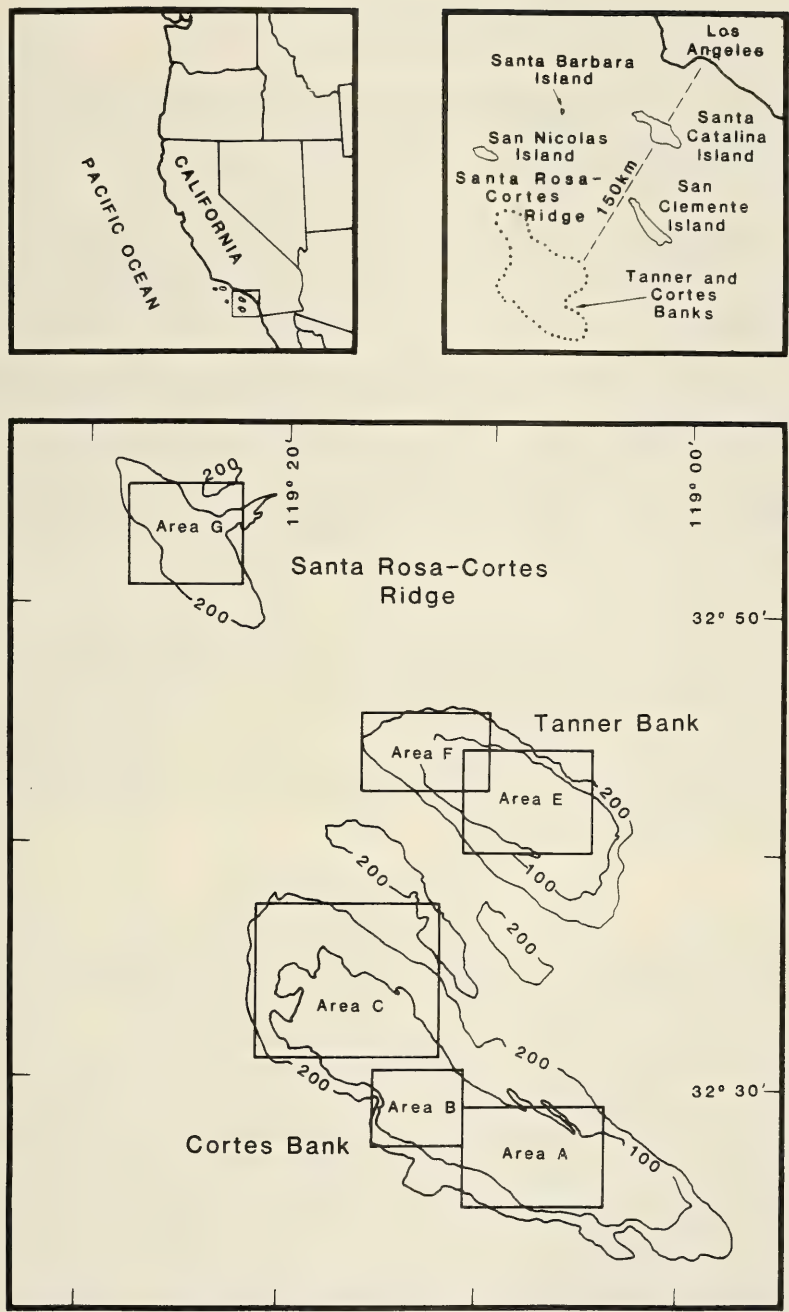


Fig. 1. Map of Tanner and Cortes Banks and Santa Rosa-Cortes Ridge showing location of the six study areas (depths shown are in meters).

Cortes Ridge (IEC 1979). This area consists of numerous small outcrops rising above flattened ridge tops (IEC 1979). Variable amounts of boulders, cobble, gravel, and sand cover the surface of the ridge providing a heterogeneous benthic habitat (IEC 1979).



## Materials and Methods

### Field Operations

Six areas (A, B, C, E, F, and G) corresponding to general geologic regions of the banks and ridge were surveyed (Fig. 1). Survey depths on the banks ranged from 10 to 150 m and depths on the ridge ranged from 100 to 140 m.

Detailed bathymetric and geomorphologic surveys of the six areas were conducted using an EDO fathometer and a Klein 400 series side scan sonar aboard the R/V VELERO IV. Data from this survey were used to construct bathymetric base maps (2 to 5 m depth intervals) showing the types of substrates. Information from these maps was used to position thirty-seven transects for the subsequent submersible survey.

The NEKTON (Gamma) two-person submersible and the support ship SEAMARK were used for the submersible survey. A Cubic Western Data model DM-54 ARGO navigation system was used to provide range-range fixes during the surveys; a Motorola Mini-Ranger III radio positioning system was used for backup and calibration of the primary system. Navigational accuracy was estimated to be  $\pm 5$  m. The position and course of the submersible were corrected relative to the support vessel by estimating the range and bearing to a surface buoy towed by the submersible.

Biological data collected during the survey included observer records (continuous tape-recorded commentary, notes, and 35 mm still photographs), continuous black and white video, and 35 mm photographs taken with a Benthos camera set to photograph at approximately 10 m intervals along the transects. Clocks on the bridge of the support vessel, inside the submersible, and within the data chamber of the Benthos camera were intercalibrated to provide cross referencing of all data records and navigational positions.

### Data Analysis

Observer records, video, and still photographs were catalogued according to geographic location (latitude and longitude), time of observation, depth, substrate, and species present and their respective densities. Densities of species for which individuals could not be easily distinguished (e.g., algal turfs or crusts) were expressed as percent cover; all other species were estimated as numbers of individuals/m<sup>2</sup>. Only organisms larger than approximately 2 cm were identified from the data records; no samples or rock scrapings were collected. Identification of species from photographs was verified by various taxonomic specialists.

Densities of organisms only were obtained from 35 mm slides that represented areas of sea-bottom of approximately 1 m<sup>2</sup>. The area covered by each photograph was estimated based on the distance between the camera and substratum, and on sizes of certain organisms (e.g., cup corals) within the area. Absolute values of densities were not used because of error associated with our areal estimates; rather, data for each species were divided into categories of relative abundance (e.g., very abundant, abundant, common, sparse). The remaining photographic and observational information was used only to determine the presence of species.

Taxonomic similarity between the six areas was calculated from presence-absence data using the Czekanowski coefficient, and dendrograms were compiled using a group average sorting strategy (Clifford and Stephenson 1975). Classifi-

cation analyses were conducted on four groups of data (invertebrates, algae, fish, and all organisms combined) to determine if similar patterns emerged for different types of organisms.

To determine changes in the dominance of particular species with increasing depth, the relative abundance of selected dominant species was tabulated at 6 m depth intervals. Different assemblages of organisms were determined subjectively from this table.

The time spent at various depths varied greatly (Table 1). Less time was spent in the deepest areas (> 140 m) compared with mid-depth areas (around 60 to 70 m). Consequently, estimated densities of species might be biased because of the unequal number of observations at each depth interval. (An observation represented a single notation made by an observer, a still photograph, or a video record.) To overcome this potential bias, abundance data were standardized by calculating a percentage of occurrence (*P*) for each dominant species at each depth interval. For example, if the total number of observations of all species at a depth interval was 100, a species observed five times at that interval would have a *P* value of 0.05. A better estimate of species abundance can be determined by comparing its

Table 1. Number of observations made at 6 m (approximately 20 ft) depth intervals in each survey area.

| Depth group<br>(m)                                    | Area |     |     |     |     |     | Total obs.<br>per group |
|-------------------------------------------------------|------|-----|-----|-----|-----|-----|-------------------------|
|                                                       | A    | B   | E   | C   | F   | G   |                         |
| 12-18                                                 | 35   | 9   | —   | —   | —   | —   | 44                      |
| 18-24                                                 | 68   | 27  | —   | —   | —   | —   | 95                      |
| 24-30                                                 | 67   | 70  | —   | —   | —   | —   | 137                     |
| 30-36                                                 | 107  | 45  | 21  | —   | —   | —   | 173                     |
| 36-42                                                 | 67   | 45  | 53  | —   | —   | —   | 165                     |
| 42-49                                                 | 70   | 34  | 65  | —   | —   | —   | 169                     |
| 49-55                                                 | 147  | 37  | 102 | —   | 15  | —   | 301                     |
| 55-61                                                 | 127  | 48  | 105 | —   | 17  | —   | 297                     |
| 61-67                                                 | 86   | 126 | 129 | 25  | 40  | —   | 406                     |
| 67-73                                                 | 72   | 34  | 66  | 14  | 76  | —   | 262                     |
| 73-79                                                 | 77   | 42  | 126 | 32  | 82  | —   | 359                     |
| 79-85                                                 | 28   | 61  | 187 | 59  | 34  | —   | 369                     |
| 85-91                                                 | 3    | 37  | 33  | 158 | 46  | —   | 277                     |
| 91-97                                                 | —    | 2   | 7   | 121 | 34  | —   | 164                     |
| 97-103                                                | —    | —   | —   | 24  | 23  | 30  | 77                      |
| 103-110                                               | —    | —   | —   | 36  | 19  | 48  | 103                     |
| 110-116                                               | —    | —   | —   | 29  | 17  | 71  | 117                     |
| 116-122                                               | —    | —   | —   | 10  | 32  | 20  | 62                      |
| 122-128                                               | —    | —   | —   | —   | 2   | 12  | 14                      |
| 128-134                                               | —    | —   | —   | —   | 4   | 7   | 11                      |
| 134-140                                               | —    | —   | —   | —   | 23  | 1   | 24                      |
| 140-146                                               | —    | —   | —   | —   | 23  | —   | 23                      |
| 146-152                                               | —    | —   | —   | —   | 1   | —   | 1                       |
| Total observations per area                           |      |     |     |     |     |     |                         |
|                                                       | 954  | 617 | 894 | 508 | 488 | 189 | 3650                    |
| Percentage of total observations<br>for entire survey |      |     |     |     |     |     |                         |
|                                                       | 26   | 17  | 24  | 14  | 13  | 5   |                         |



*P* value and its relative abundance at a particular depth interval. From the previous example, if a low *P* value is coupled with high abundance, then the species occurs in dense patches.

### Results

A total of 52 nmi was surveyed along the 37 transects in the six study areas. Data were collected from over 8000 35 mm color slides and approximately 60 hours of observer and video records.

Three hundred and three taxa were observed, representing 34 species of algae, 181 species of invertebrates, and 88 species of fish (Appendix available from the authors). Several taxa included groups of species whose specific identifications could not be determined either from direct observations or photographs (e.g., dichotomous-flabellate red algae), or are poorly known (e.g., Demospongia). The greatest number of taxa was observed in Area A (198), followed by Areas E (180), B (162), F (137), C (133), and G (65). Algae were most commonly represented by the rhodophytes (18 taxa). The most common invertebrate groups were coelenterates (49 taxa) and molluscs and echinoderms (38 taxa each). Fish were most commonly represented by rockfish (31 taxa) and surfperch (9 taxa).

Classification analyses indicated that the same groupings of areas (Areas A, B and E; Areas C and F; and Area G) emerged after analysis of each of the four data sets (Fig. 2). The percent similarity within each group over all data sets was moderate to high ( $\geq 0.657$ ).

Areas were grouped along a depth gradient based on classification. Areas A, B, and E were the shallowest sites, Areas C and F generally were intermediate, and Area G was deepest. The three groups of areas reflected the distribution of many taxa along a depth gradient. For example, many species of algae such as *Cystoseira* and *Eisenia* were restricted to shallow areas (Areas A, B, and E), whereas echinoderms such as *Florometra* and *Gorgonocephalus* were found only at deeper sites (Areas C and F; Area G). Groupings among the areas also may be influenced by the number of observations taken (Table 1). For example, 67% of all observations made during the study came from Areas A, B, and E (Table 1). Therefore, the chance of observing more species, and consequently the potential for a higher degree of similarity, was greater among these three areas.

For the gradient analysis (Fig. 3), information on densities of 26 dominant taxa for the six areas was pooled for each depth interval. Pooling was necessary to show the complete depth range for a given taxon; it is likely that the depth distributions of some taxa would be broader than the range of depths sampled in a single area, or groups of areas derived from the classification analysis.

Relative abundance (sparse, common, abundant, and very abundant) along with *P* values for specific depth intervals are presented for the dominant taxa in Figure 3; Table 2 gives a key to the estimated range of densities represented by these categories for each taxon. In general, high densities of a taxon were associated with high *P* values, while low abundances corresponded with low *P* values.

Patterns of abundance displayed by taxa in Figure 3 suggest that at least four depth-related assemblages of organisms were present in the study area (Table 3). These groups have relatively distinct depth ranges that correspond to intervals of peak abundance of the dominant taxa; however, as shown in Figure 3, the depth range of each taxon usually extended over more than one community.

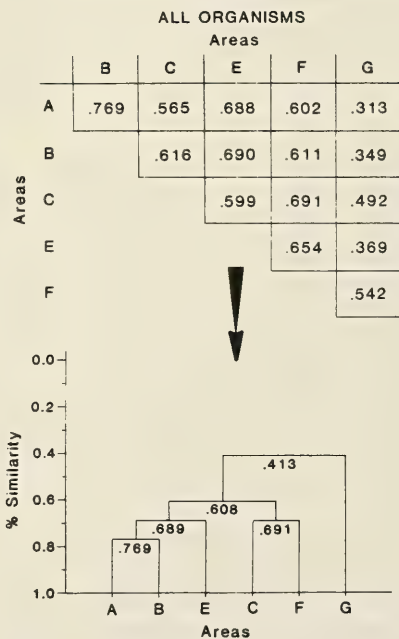
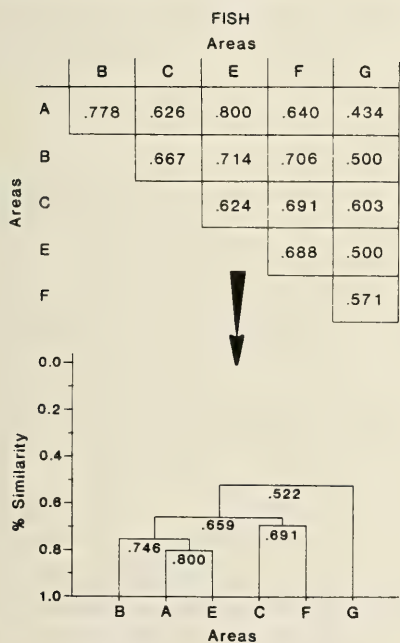
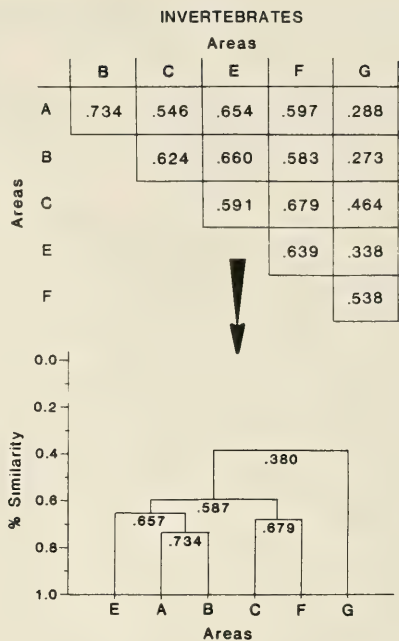
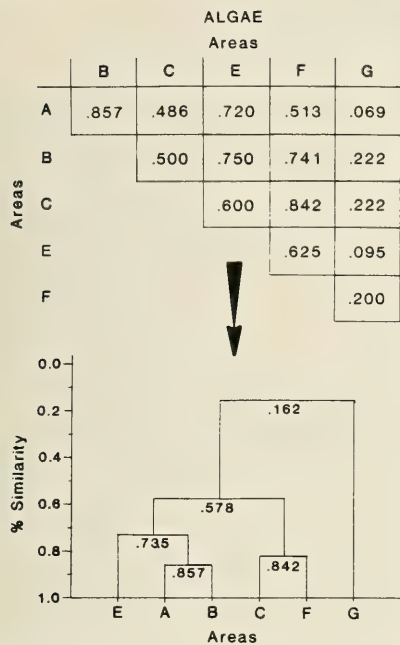


Fig. 2. Classification analysis for algae, invertebrates, fish, and the total of all organisms combined. Similarity indices were calculated using the Czekanowski coefficient, and dendrograms were constructed using the group average sorting strategy.



| Taxon                              | Depth Intervals (m) |        |        |        |        |        |        |        |        |        |        |        |        |        |        |         |         |         |
|------------------------------------|---------------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|---------|---------|---------|
|                                    | 12-16               | 16-24  | 24-30  | 30-36  | 36-42  | 42-48  | 48-54  | 54-61  | 61-67  | 67-73  | 73-79  | 79-86  | 86-91  | 91-97  | 97-103 | 103-110 | 110-116 | 116-122 |
| <i>Eisenia arborea</i>             | ● (91)              | ● (83) | ☆ (72) | ☆ (68) | ☆ (33) | ☆ (14) | ☆ (3)  | ☆ (3)  | ☆ (5)  |        | ● (3)  | ● (3)  |        |        |        |         |         |         |
| <i>Bosellia/ Calliarthron</i> spp. | +                   | +      | ☆ (52) | ☆ (73) | ☆ (91) | ☆ (91) | ☆ (64) | ☆ (70) | ☆ (27) | ● (7)  | ● (2)  | ● (3)  | ● (4)  |        |        |         |         |         |
| <i>Gelidium</i> spp.               | +                   | ☆ (18) | ☆ (4)  | ☆ (1)  | ☆ (2)  |        | ☆ (3)  | ☆ (7)  | ☆ (5)  |        |        |        |        |        |        |         |         |         |
| <i>Semicossyphus pulcher</i>       | ● (34)              | +      | +      | +      | +      | ☆ (14) | ☆ (20) | ☆ (6)  | ☆ (7)  | ☆ (5)  | ☆ (6)  | ☆ (5)  | ☆ (8)  | ☆ (7)  |        |         |         |         |
| <i>Oxyjulis californica</i>        | ☆ (68)              | ☆ (58) | ☆ (57) | ● (42) | ● (34) | ☆ (34) | ☆ (28) | ☆ (20) | ☆ (17) | ☆ (9)  | ☆ (11) | ☆ (4)  | ☆ (3)  | ☆ (6)  | ☆ (1)  |         |         |         |
| <i>Laminaria farlowii</i>          | ☆ (25)              | +      | ☆ (28) | ☆ (43) | ☆ (35) | ☆ (39) | ☆ (24) | ☆ (16) | ☆ (8)  | ☆ (5)  | ☆ (1)  | ☆ (8)  | ☆ (4)  |        |        |         |         |         |
| <i>Agarum fimbriatum</i>           | +                   | +      | ☆ (22) | ☆ (59) | ☆ (55) | ☆ (74) | ☆ (67) | ☆ (50) | ☆ (20) | ☆ (5)  | ☆ (3)  |        |        |        |        |         |         |         |
| <i>Allopora californica</i>        |                     | ☆ (5)  | ☆ (7)  | ☆ (26) | ☆ (13) | ☆ (12) | ☆ (22) | ☆ (10) | ☆ (4)  | ☆ (4)  | ☆ (3)  | ☆ (3)  | ☆ (1)  | ☆ (5)  | ☆ (6)  | ☆ (8)   |         |         |
| <i>Paracystus stearnsi</i>         | ● (2)               | ● (2)  | ☆ (7)  | ☆ (14) | ☆ (26) | ☆ (21) | ☆ (22) | ☆ (36) | ☆ (38) | ☆ (9)  | ☆ (19) | ☆ (15) | ☆ (16) | ☆ (17) | ☆ (10) | ☆ (17)  | ☆ (6)   |         |
| Encrusting coralline algae         | +                   | ☆ (61) | ☆ (67) | ☆ (76) | ☆ (75) | ☆ (83) | ☆ (75) | ☆ (81) | ☆ (69) | ☆ (56) | ☆ (43) | ☆ (63) | ☆ (66) | ☆ (60) | ☆ (68) | ☆ (75)  | ☆ (35)  | ☆ (79)  |
| <i>Patiria miniata</i>             | ☆ (7)               | ☆ (19) | ☆ (2)  | ☆ (13) | ☆ (21) | ☆ (20) | ☆ (20) | ☆ (14) | ☆ (12) | ☆ (6)  | ☆ (4)  | ☆ (3)  | ☆ (2)  | ☆ (6)  | ☆ (1)  |         |         |         |
| <i>Eugorgia rubens</i>             |                     | ☆ (11) | ☆ (2)  | ☆ (6)  | ☆ (1)  | ☆ (12) | ☆ (22) | ☆ (10) | ☆ (9)  | ☆ (9)  | ☆ (2)  | ☆ (4)  | ☆ (1)  | ☆ (1)  |        |         |         |         |
| <i>Sebastes hopkinsi</i>           | ● (5)               | ☆ (13) | ☆ (14) | ☆ (31) | ☆ (28) | ☆ (52) | ☆ (43) | ☆ (48) | ☆ (50) | ☆ (53) | ☆ (30) | ☆ (21) | ☆ (43) | ☆ (35) | ☆ (21) | ☆ (46)  | ☆ (17)  | ☆ (5)   |
| <i>Sebastes</i> spp.               | ☆ (3)               | ☆ (28) | ☆ (26) | ☆ (17) | ☆ (35) | ☆ (40) | ☆ (31) | ☆ (37) | ☆ (39) | ☆ (45) | ☆ (37) | ☆ (30) | ☆ (44) | ☆ (29) | ☆ (31) | ☆ (49)  | ☆ (48)  | ☆ (32)  |
| <i>Sebastes rooseae</i>            | ☆ (1)               | ☆ (4)  | ☆ (6)  | ☆ (12) | ☆ (6)  | ☆ (10) | ☆ (11) | ☆ (9)  | ☆ (10) | ☆ (6)  | ☆ (4)  | ☆ (4)  | ☆ (4)  | ☆ (3)  | ☆ (1)  | ☆ (2)   | ☆ (5)   | ☆ (14)  |
| <i>Sebastes constellatus</i>       |                     | ☆ (7)  | ☆ (2)  | ☆ (2)  | ☆ (3)  | ☆ (4)  | ☆ (8)  | ☆ (7)  | ☆ (8)  | ☆ (6)  | ☆ (2)  | ☆ (3)  | ☆ (2)  | ☆ (16) | ☆ (3)  |         |         | ☆ (4)   |
| <i>Mediaster aequalis</i>          | ☆ (1)               | ☆ (7)  | ☆ (15) | ☆ (16) | ☆ (14) | ☆ (11) | ☆ (28) | ☆ (27) | ☆ (34) | ☆ (40) | ☆ (40) | ☆ (17) | ☆ (18) | ☆ (13) | ☆ (11) | ☆ (9)   | ☆ (10)  | ☆ (4)   |
| <i>Balanophyllia elegans</i>       | ☆ (5)               | ☆ (6)  | ☆ (17) | ☆ (6)  | ☆ (5)  | ☆ (5)  | ☆ (5)  | ☆ (9)  | ☆ (5)  | ☆ (17) | ☆ (12) | ☆ (16) | ☆ (27) | ☆ (38) | ☆ (10) | ☆ (13)  | ☆ (11)  | ☆ (2)   |
| <i>Maripelta rotata</i>            |                     |        |        |        |        | ☆ (3)  | ☆ (3)  | ☆ (6)  | ☆ (15) | ☆ (7)  | ☆ (2)  | ☆ (2)  |        |        |        |         | ☆ (2)   |         |
| ? <i>Clathrina</i> sp.             |                     |        |        | ☆ (6)  |        |        |        | ☆ (2)  | ☆ (6)  | ☆ (20) | ☆ (9)  | ☆ (9)  | ☆ (10) | ☆ (3)  | ☆ (5)  | ☆ (1)   | ☆ (9)   | ☆ (2)   |
| <i>Heterogorgia papillosa</i>      |                     |        |        |        | ☆ (5)  |        |        | ☆ (5)  | ☆ (6)  | ☆ (3)  | ☆ (2)  | ☆ (7)  |        |        |        |         |         |         |
| <i>Lytechinus anamesus</i>         |                     | ☆ (7)  | ☆ (3)  | ☆ (8)  | ☆ (13) | ☆ (22) | ☆ (19) | ☆ (25) | ☆ (25) | ☆ (34) | ☆ (39) | ☆ (19) | ☆ (8)  |        | ☆ (5)  | ☆ (17)  | ☆ (19)  | ☆ (18)  |
| <i>Sebastes levis</i>              |                     |        | ☆ (5)  | ☆ (6)  | ☆ (3)  | ☆ (1)  | ☆ (1)  | ☆ (2)  | ☆ (1)  | ☆ (3)  | ☆ (1)  | ☆ (2)  | ☆ (6)  | ☆ (2)  | ☆ (8)  |         |         | ☆ (4)   |
| <i>Plumarella longispina</i>       |                     |        |        | ☆ (6)  | ☆ (3)  | ☆ (1)  | ☆ (9)  | ☆ (9)  | ☆ (10) | ☆ (12) | ☆ (23) | ☆ (12) | ☆ (5)  | ☆ (17) | ☆ (8)  | ☆ (10)  | ☆ (7)   | ☆ (9)   |
| ? <i>Staurocalyptus</i> sp.        |                     |        |        | ☆ (1)  |        | ☆ (3)  | ☆ (2)  | ☆ (5)  | ☆ (5)  | ☆ (5)  | ☆ (10) | ☆ (10) | ☆ (13) | ☆ (6)  | ☆ (5)  | ☆ (5)   | ☆ (14)  | ☆ (9)   |
| <i>Florometra serratifidissima</i> |                     |        |        |        |        |        |        |        |        |        |        | ☆ (5)  | ☆ (13) | ☆ (44) | ☆ (62) | ☆ (87)  | ☆ (61)  | ☆ (96)  |

● Very Abundant  
☆ Abundant

+ Common  
● Sparse

(F) % of observations at that depth interval

Fig. 3. Distribution of common taxa among depths surveyed.

A shallow-water assemblage characterized by the southern sea palm *Eisenia arborea* and erect coralline algae predominated from at least 14 to about 40 m depth. *Eisenia arborea* commonly occurred in densities of 4 to 6 individuals/m<sup>2</sup>; coralline algae reached nearly 100% coverage along some transects. Locally abundant subdominant taxa included the red alga *Gelidium* spp., various brown algae (*Agarum fimbriatum*, *Laminaria farlowii*, and *Zonaria farlowii*), and in some protected areas, the brittle star *Ophiothrix spiculata*. Suspension-feeding invertebrates such as bryozoans, sponges, and coelenterates were abundant throughout the community, but were often partially obscured by thick algal cover. Common fish included opaleye *Girella nigricans*, rockfish (*Sebastes mystinus* and *S. hopkinsi*),

Table 2. Key to relative abundance data presented in Fig. 3.

| Taxon                               | Sparse | Common | Abundant | Very abundant |
|-------------------------------------|--------|--------|----------|---------------|
| <i>Eisenia arborea</i>              | <1     | 1      | 2-3      | >3            |
| <i>Bossiaella/Calliarthron</i> spp. | 5%     | 5-50%  | 50-80%   | >80%          |
| <i>Gelidium</i> spp.                | <5%    | 5-50%  | 50-80%   | >80%          |
| <i>Semicossyphus pulcher</i>        | 1      | 2-5    | 6-10     | —             |
| <i>Oxyjulis californica</i>         | 1-10   | 11-100 | 100-1000 | >1000         |
| <i>Laminaria farlowii</i>           | <1     | 1      | 2-3      | >3            |
| <i>Agarum fimbriatum</i>            | <1     | 1      | 2-3      | >3            |
| <i>Allopora pacifica</i>            | <1     | 1      | ≥2       | —             |
| <i>Paracyathus stearnsi</i>         | 1-4    | 5-10   | 11-20    | >20           |
| Encrusting coralline algae          | <5%    | 5-50%  | 50-80%   | 80%           |
| <i>Patiria miniata</i>              | 1      | 1      | 2-3      | >3            |
| <i>Eugorgia rubens</i>              | <1     | 1      | 2-3      | >3            |
| <i>Sebastes hopkinsi</i>            | 1-10   | 11-50  | 51-100   | >100          |
| <i>Sebastes</i> spp.                | 1      | 2-4    | 5-10     | >10           |
| <i>Sebastes rosaceus</i>            | 1      | 2-4    | 5-10     | >10           |
| <i>Sebastes constellatus</i>        | 1      | 2-5    | >5       | —             |
| <i>Mediaster aequalis</i>           | <1     | 1      | 2-3      | >3            |
| <i>Balanophyllia elegans</i>        | 1-4    | 5-10   | 11-20    | >20           |
| <i>Maripelta rotata</i>             | 1-2    | 3-5    | >5       | —             |
| ? <i>Clathrina</i> sp.              | <1     | 1      | 2-3      | >3            |
| <i>Heterogorgia papillosa</i>       | 1-2    | 3-5    | 5        | —             |
| <i>Lytechinus anamesus</i>          | 1-2    | 3-10   | 11-20    | >20           |
| <i>Sebastes levis</i>               | 1      | >1     | —        | —             |
| <i>Plumarella longispina</i>        | <1     | 1      | 2-3      | >3            |
| ? <i>Staurocalyptus</i> sp.         | <1     | 1      | 2-3      | >3            |
| <i>Florometra serratissima</i>      | 1      | 2-10   | 10-30    | >30           |

and blackeye gobies *Coryphopterus nicholsii*. The shallow-water *Eisenia* assemblage graded into an intermediate-depth (40 to 60 m) assemblage characterized by broad-bladed brown algae (*Agarum fimbriatum* and *Laminaria farlowii*). These species commonly attained densities of over 3 individuals/m<sup>2</sup>, representing nearly 100% cover in some areas. Other abundant taxa in this assemblage included erect coralline algae, the brown alga *Zonaria farlowii*, the sea fan *Eugorgia rubens*, and the sea stars *Patiria miniata* and *Mediaster aequalis*. In addition to several species of fish from the shallower *Eisenia* community, species such as the ocean whitefish *Caulolatilus princeps* and the rockfish *Sebastes serranoides* and *S. paucispinis* were abundant. Rockfish generally were more common than in the shallow-water areas.

Below approximately 60 to 90 m depth, erect macroalgae were sparse and encrusting coralline algae were the dominant growth form, reaching almost 100% cover in many areas. Encrusting coralline algae also were abundant in the shallower areas, however, encrusting organisms often were obscured by thick algal cover. Subdominants in the assemblage included the gorgonian *Plumarella longispina*, the sea star *Mediaster aequalis* and several types of sponges including ?*Clathrina* sp. and ?*Staurocalyptus* sp. Other common organisms included various unidentified red, green, orange, tan, and yellow crusts, probably representing bryozoans, sponges, tunicates, and algae. Rockfish were common, particularly *Sebastes rosaceus* and *S. constellatus*.



Table 3. Biological assemblages and subdominant taxa observed on Tanner and Cortes banks and the Santa Rosa-Cortes Ridge.

| Assemblage                                           | Depth range (m) | Subdominant taxa                                                                                                                        |
|------------------------------------------------------|-----------------|-----------------------------------------------------------------------------------------------------------------------------------------|
| <i>Eisenia arborea</i> /erect coralline algae        | 14-40           | <i>Gelidium</i> spp.<br><i>Laminaria farlowii</i><br><i>Agarum fimbriatum</i><br><i>Ophiothrix spiculata</i><br><i>Zonaria farlowii</i> |
| <i>Agarum fimbriatum</i> / <i>Laminaria farlowii</i> | 40-60           | <i>Zonaria farlowii</i><br>erect coralline algae<br><i>Eugorgia rubens</i><br><i>Mediaster aequalis</i><br><i>Patiria miniata</i>       |
| Encrusting coralline algae                           | 60-90           | <i>Plumarella longispina</i><br><i>Mediaster aequalis</i><br>sponges                                                                    |
| <i>Florometra serratissima</i> /ophiuroids           | 90-150          | —                                                                                                                                       |

The deepest assemblage occurred from 90 to at least 150 m depth and was characterized by high abundances of the feather star *Florometra serratissima* and several species of brittle stars (?*Ophiopsila* sp. and ?*Ophiopholis*?*Ophiocantha* sp.). This assemblage was found primarily on Santa Rosa-Cortes Ridge (Area G) but also occurred in deeper areas of Tanner and Cortes Banks. Other common species included the basketstar *Gorgonocephalus caryi*, sponges, the sea anemone *Actinostola* sp., rockfish (primarily *Sebastes chlorostictus*/*rosenblatti*), and ratfish *Hydrolagus collieri*.

Several species observed in the study area exhibited broad depth ranges that exceeded published depth records (Table 4). Additionally, a southern range extension was noted for the tiger rockfish *Sebastes nigrocinctus*, and a northern extension for the fish Family Opistognathidae (Gotshall pers. comm.).

### Discussion

The dominant taxa and diversity of plants and animals observed during the survey of the Tanner and Cortes Banks and Santa Rosa-Cortez Ridge were similar to those in other communities found in rocky subtidal habitats in the Southern California Bight. However, the relative abundances of certain species were often greater on the banks, and many species were distributed over a wider depth range compared with other areas around the Channel Islands and along the mainland. Conversely, species such as the algae *Cystoseira*, *Macrocystis*, and *Pterygophora* were less abundant than in other areas in the Bight.

The lower depth limit of the shallow-water *Eisenia*/erect coralline algae assemblage was approximately 40 m on the banks (Table 3, Fig. 3); this bathymetric range is similar to the lower limits of *Eisenia* assemblages on several of the Channel Islands (approximately 30 to 49 m depth; J. Engle pers. comm.), but was much deeper than the populations found along the mainland (5 m depth; J. Word, M. Moore, L. Harris pers. comm.). During previous studies on the banks (Smith et al. 1975; Littler et al. 1978; Lewbel et al. 1981), the *Eisenia* assemblage was

Table 4. Deepest depth of occurrence of selected taxa from Tanner and Cortes banks.

| Species                                | Maximum depth recorded for study (m) | Previous record (m) (references) |
|----------------------------------------|--------------------------------------|----------------------------------|
| Algae                                  |                                      |                                  |
| <i>Codium</i> sp. (encrusting)         | 91                                   | 25 (Abbott and Hollenberg 1976)  |
| <i>Eisenia arborea</i>                 | 79                                   | 10 (Abbott and Hollenberg 1976)  |
| <i>Laminaria farlowii</i>              | 131                                  | 50 (Abbott and Hollenberg 1976)  |
| <i>Zonaria farlowii</i>                | 91                                   | 20 (Abbott and Hollenberg 1976)  |
| <i>Bossiaella/Calliarthron</i> spp.    | 91                                   | 46 (Abbott and Hollenberg 1976)  |
| <i>Gelidium</i> spp.                   | 61                                   | 30 (Abbott and Hollenberg 1976)  |
| <i>Maripelta rotata</i>                | 112                                  | 30 (Abbott and Hollenberg 1976)  |
| <i>Botryocladia pseudodichotoma</i>    | 105                                  | 38 (Abbott and Hollenberg 1976)  |
| Coelenterates                          |                                      |                                  |
| <i>Allopora californica</i>            | 98                                   | 53 (Gotshall and Laurent 1979)   |
| <i>Lophogorgia chilensis</i>           | 77                                   | 61 (Gotshall and Laurent 1979)   |
| Echinoderms                            |                                      |                                  |
| <i>Strongylocentrotus franciscanus</i> | 113                                  | 90 (Morris et al. 1980)          |
| <i>Pisaster giganteus</i>              | 90                                   | 88 (Fisher 1930)                 |
| Fish                                   |                                      |                                  |
| <i>Oxyjulis californica</i>            | 101                                  | 101 (Gotshall 1981)*             |
| <i>Semicossyphus pulcher</i>           | 88                                   | 88 (Gotshall 1981)*              |
| <i>Chromis punctipinnis</i>            | 82                                   | 82 (Gotshall 1981)*              |

\* Depth record in this reference recorded from present study.

observed to about 25 m depth; its deeper occurrence in the present study probably was a function of the much greater area surveyed compared with earlier studies. The subdominant *Ophiothrix spiculata* occurred at densities comparable to certain locations between 20 and 25 m around Santa Barbara Island (J. Engle pers. comm.).

The *Agarum/Laminaria* assemblage occurred from approximately 40 to 60 m depth (Table 3, Fig. 3). Ecomar, Inc. (1978) noted a similar distribution (40 to 55 m depth) for *Agarum* on the Tanner Bank. Around Santa Catalina Island, *Agarum* and *Laminaria* occur from 20 to 40 m and are often intermixed with *Eisenia* and coralline algae (R. Given pers. comm.); the separation between these two assemblages on Catalina is less distinct than on the banks. At least two subdominant species (*Eugorgia rubens* and *Mediaster aequalis*) prevalent in the *Agarum/Laminaria* assemblage on the banks (Table 3) also occur at Catalina Island at comparable depths (J. Engle pers. comm.). However, the other subdominant species were distributed at much greater depths on the banks.

Encrusting coralline algae were common to abundant in all assemblages (Fig. 3), and were co-dominant or subdominant at most depths. These taxa dominated from 60 to 90 m where they almost completely covered the substrate, but the abundance and size of erect macroalgae was sharply reduced. Subdominants in this assemblage (Table 3) also are present along the mainland and at Catalina Island but not in the same relative abundances (R. Given, J. Word, M. Moore, L. Harris pers. comm.).





Fig. 4. Typical hard-bottom community observed in water depths >90 m. Species present include (1) the basket star *Gorgonocephalus caryi*, (2) the anemone *Actinostola* sp., (3) the feather star *Florometra serratissima*, (4) ophiuroids ?*Ophiopholis*/?*Ophiocantha* and ?*Ophiopsila*, and (5) rockfish *Sebastes* spp.

The deepest assemblage (90 to at least 150 m depth) was dominated by the feather star *Florometra serratissima* and several species of ophiuroids (?*Ophiopholis*/?*Ophiocantha* spp. and ?*Ophiopsila* sp.) (Fig. 4). This assemblage was found mainly on the ridge (Area G) and deeper portions of the banks (Areas C and F). In Area G the basketstar *Gorgonocephalus caryi* was common and often occurred near the tops of rock pinnacles.

This association of echinoderms is known from other deep-water areas of the Bight (J. Word, pers. comm.) but has not been described previously as an assemblage. During recent surveys conducted on hard-bottom areas near Point Conception, California (Nekton, Inc. 1981; Dames and Moore 1982), photographs were taken at depths down to 500 m of assemblages we believe correspond with the *Florometra*/ophiuroid community described here. In these studies *Florometra* was reported as the dominant species with the ophiuroids *Ophiocantha* sp. and *Ophiopholis* sp. as subdominants. Although qualitative, our review of video tapes from Point Conception studies indicated that populations of *Florometra* were not as dense as on Tanner and Cortes Banks and Santa Rosa-Cortes Ridge. Recent (July 1984) manned submersible surveys conducted by SAIC in the Santa Maria Basin recorded several areas of dense assemblages of *Florometra*, *Ophiocantha* and other ophiuroid species.

Many species of feather stars commonly occur in dense aggregations probably resulting from the poor dispersal abilities of their larvae and settlement near the adults (Hyman 1955). However, *Florometra serratissima* larvae exhibit good dis-

persal abilities and aggregations may provide higher success rates of fertilization (Mladenov and Chia 1983). Populations of feather stars are maintained by suspended food resources (Liddell 1982; Meyer 1982); the dense aggregations of *Florometra* in the study area may be maintained by a rich supply of suspended material settling downward from shallower areas.

Species common in the deep-water areas investigated by Nekton, Inc. (1981), Dames and Moore (1982) and this study included sponges *Staurocalyptus* sp. and *Leucetta* sp., the solitary coral *Paracyathus stearnsi*, the basketstar *Gorgonocephalus caryi*, various rockfish (*Sebastes* spp.), lingcod *Ophiodon elongatus*, poachers (Agonidae), combfish (Zaniolepidae), and the ratfish *Hydrolagus colliei*.

Several species common around the Channel Islands and rocky areas of the mainland were conspicuously absent on the banks and ridge: giant kelp *Macrocystis pyrifera*, gorgonians *Muricea californica* and *M. fruticosa*, kelp bass *Paralabrax clathratus*, and garibaldi *Hypsypops rubicundus*. The majority of algal species on the banks are low-growing forms with strong holdfasts able to withstand dislodgement during storms. Cowen et al. (1982) and Moreno and Sutherland (1982) have shown storm damage to be a primary factor in structuring *Macrocystis* communities. Therefore, heavy swell and currents over the banks may prevent the formation of *Macrocystis* beds. Populations of *Muricea* spp. may be limited by cold water and/or poor dispersal abilities of the larvae (R. Grigg, pers. comm.). The low abundance of *Paralabrax* and *Hypsypops* may be related to lack of suitable habitat and the prevalence of colder water (both species are warm temperate or subtropical).

The extended depth ranges of many species, especially macroalgae, on the banks and ridge probably result from the locally unique oceanographic conditions. The lower bathymetric distribution of macroalgae such as *Macrocystis* is mainly a function of light and nutrients (North 1971; Druehl 1972; Jackson 1977; Gerard 1982). At nearshore sites, the development of deeper macroalgal communities can be limited by reduced light penetration caused by coastal runoff of terrigenous material. The banks and ridge are located over 100 km from shore, and consequently are somewhat isolated from many coastal influences. Water visibility often is greater than 20 m as noted both during this survey and by Lewbel et al. (1981).

Wave and surge activity might result in a deeper mixed layer having higher concentrations of oxygen and food. Although direct data are not available, we suggest that the combination of these physical factors might enhance benthic productivity and enable macroalgae and associated organisms to inhabit greater depths compared with other areas of the Southern California Bight.

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## Marine Hydroid Assemblages in Soft-Bottom Habitats on the Hueneme Shelf off Southern California, and Factors Influencing Hydroid Distribution

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**Abstract.**—Twenty-five marine hydroid species were encountered in studies on Hueneme Shelf. Fourteen species appear to occur primarily in areas of soft substrates. These species exhibited distinct patterns in depth distribution and specific substrate preference. *Clytia bakeri* and *Phialella ?rugosa* characterized the shallow region of the study area (3 to 11 m), *Tubularia* sp. A, *Plumularia alicia*, *Hydrallmania distans*, *Aglaophenia dispar*, *Clytia universitatis*, and *Lovenella nodosa* characterized the mid-depths (11 to 33 m), and *Plumularia mobilis*, *Monobrachium parasitum*, *Thuiaria ?alba*, *Euphysa* sp., *Corymorpha palma*, and *Aglaophenia lophocarpa* characterized the deeper region (24 to 60 m). These patterns were stable over several years. Factors probably operative in these distribution patterns include sediment stability, availability of substrates, and food. Favored substrates were polychaete worm tubes, shells, and shell debris.

These observations constitute range extensions for eight of the species. Two species are probably undescribed. Natural history information is presented on all species.

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Our knowledge of the marine hydroid fauna of southern California issues mainly from studies by Torrey (1902 and 1904) and Fraser (1937, 1938a, b, and c, and 1948) in which they described many new species, some geographic variations, and recorded numerous range extensions. However, Torrey's (1902) remark about the absence of data concerning the natural history of the species examined is still pertinent. He commented that most west coast species had been described from preserved material lacking even rudimentary ecological information. He particularly lamented the absence of data on the nature of the substrate, and where possible he included in his papers some data on habitat, collection dates, and reproductive maturity. Fraser, on the other hand, usually presented only general data on collection locations and depths.

Hydroids are generally perceived as living on rock and shell substrates (e.g., Hyman 1940; Morris et al. 1980). It is also widely recognized that they frequently live on seaweeds (Newell 1972:8), and a small body of literature on hydroid-algal relationships has developed (see Shepherd and Watson 1970). However, reports on the occurrence of hydroids in soft-bottom habitats are uncommon and concern mainly single species. Torrey described *Corymorpha palma* from mud flats in San Diego and San Pedro bays (1902) and *Clytia bakeri* from sand beaches near San Diego (1904). Half a century later, Hand (1957) reported on the occurrence in southern California and Baja California of *Monobrachium parasitum* Meres-

chovsky, a symbiont on small deepwater clams living in mud. Hand and Jones (1957) reported an unidentified athecate hydroid from the sediments of San Francisco Bay. And finally, Jones (1961) reported on *Euphysa* sp. in the sediments of San Francisco Bay. It is recognized among hydroid specialists that genera of the Corymorphidae and several other families of athecate hydroid live anchored in sand and mud (Rees 1957:485, 521).

The intent of this paper is to report on a group of hydroids found mainly in marine soft-bottom habitats in southern California and to discuss some of the potentially important factors influencing their distribution therein. The paper is based generally on observations made from 1965 through 1975, when I had the opportunity to examine benthic assemblages on both hard and soft substrates. During the first 5 years my efforts were most intense on rocks and algae, but during the next years I worked mostly on sand and mud bottoms. Several of the species were observed primarily in areas typified by soft substrates. Factors determining distribution seem to be morphology (e.g., members of the family Corymorphidae) or distribution patterns of apparently preferred substrates.

Most of the data were obtained during two environmental studies conducted between 1971 and 1975 on the Hueneme Shelf between Hueneme and Mugu submarine canyons, approximately 80 km WNW of Los Angeles, California. The first was a study of the Southern California Edison Ormond Beach power plant from shore to a depth of 13 m (Intersea Research Corp. (IRC) 1971; Marine Biological Consultants (MBC) 1972a, b, 1973a, b, 1974a, b, 1975). The second study was done for the City of Oxnard Sanitation District during 1973 and 1974 (Environmental Quality Analysts (EQA) and MBC 1974a, b, and c; 1975a), between depths of 9 and 55 m (Fig. 1). The sediments in both study areas grade from fine sand at the 3-m depth to silty sand or sandy silt at 55 m (EQA and MBC 1975b). The shoreline is classified as semiprotected according to the criteria of Ricketts and Calvin (1968), but the area is exposed to large, long-period swells from both tropical storms and winter storms in the Gulf of Alaska (Inman 1950). Ripple marks were observed out to a depth of 27 m during winter submersible vehicle operations (EQA and MBC 1974b), indicating considerable surge activity. Also, waves breaking in at least 6-m depths have been observed during summer surveys (personal observation).

Depth-related zonation of biological assemblages was conspicuous in the study area (EQA and MBC 1975a). Between 3- and 11-m depths, a sand dollar (*Dendraster excentricus*) strongly dominated the fauna visually and in terms of biomass. Between about 11 m and 18 m, tubicolous polychaete worms (particularly *Diopatra ornata*) were visually dominant. Tubicolous polychaetes were uncommon at the 27-m stations, but two species (*Praxillura maculata* and *Lanice conchilega*) again dominated from 37 m to at least 60 m.

### Methods

This report is based mainly on data from infaunal samples and direct observation of various soft-bottom habitats. Triplicate infaunal samples were collected either by diver (1-liter sediment scrapings) or with a 0.041-m<sup>2</sup> Shipek grab sampler. Direct observations were made by observation of quadrats (1.0 or 7.5 m<sup>2</sup>) out to a depth of 18 m while diving or from 27 m out to 53 m from a two-man submersible vehicle. I made hydroid identifications either on site or in the lab-



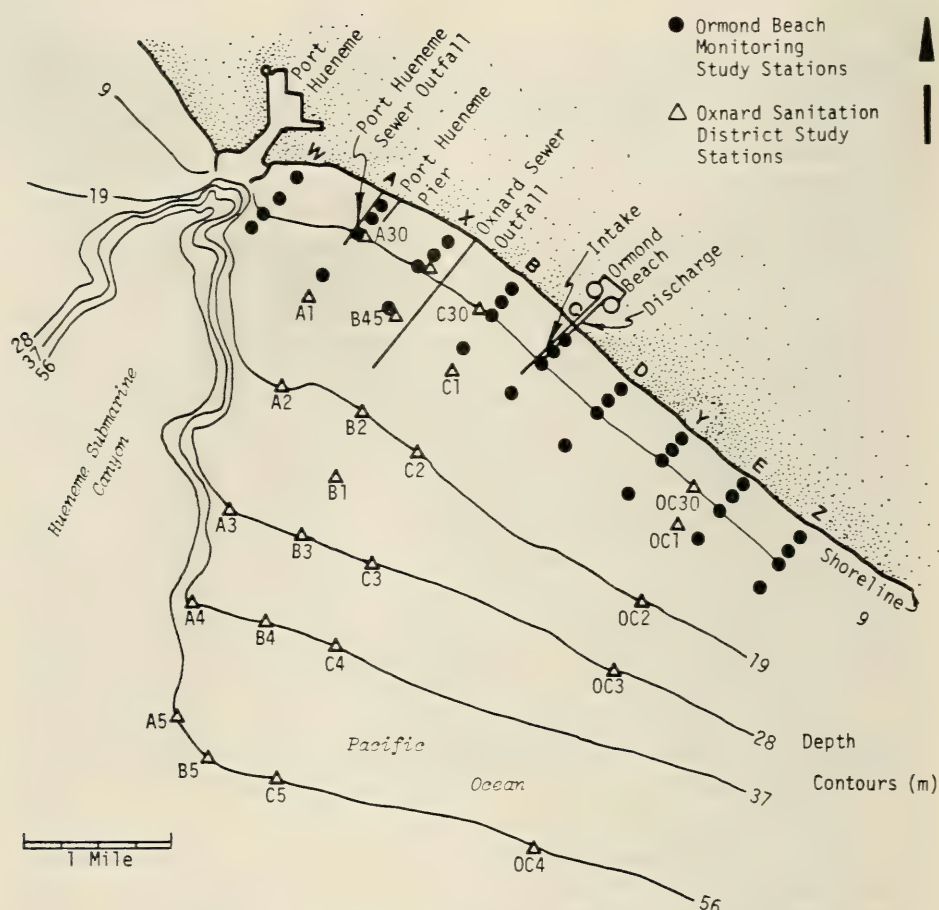


Fig. 1. Location map for studies on the Hueneme Shelf.

oratory. Quantitative data presented include density and frequency of occurrence. Density estimates are based on abundance data obtained from the infaunal samples or direct observation of quadrats (1.0 or 7.5 m<sup>2</sup>). Relative frequency was calculated to compare occurrence by depth and by survey. For comparison by depth, the value used represents the number of times a species was recorded in each depth zone divided by the total number of observations. To adjust for the difference in sampling effort between the inner and outer depth zones, a rough correction factor was employed. This practice was based on the premise that equal effort would have produced equal results at a given level in both surveys. Relative frequency of occurrence was computed for each species individually, based on the ratio of its occurrences in both surveys at depth levels where the two surveys overlapped. For instance, if a species was observed 10 times at the 12-m level in the Ormond Beach survey and five times at the same level in the Oxnard survey, the remainder of the Oxnard frequency-of-occurrence data from deeper stations was multiplied by a factor of two to adjust for the difference in effort. The adjusted frequency-of-occurrence data were then used to calculate relative frequency. Overlaps occurred in infaunal data at 7 to 11 m and in observation data at 11 to 15

m. For comparison by survey, the number of stations at which a species was observed during a survey was divided by the number of stations examined.

The strength of co-occurrence between each species pair was evaluated with the Index of Affinity ( $I_{AB}$ ) described by Southwood (1966) as adapted from Fager (1957), where:

$$I_{AB} = 2J/(A + B), \text{ and}$$

A = the number of occurrences of species A,

B = the number of occurrences of species B, and

J = the number of times the species co-occurred.

$I_{AB}$  ranges from 0 to 1.0, with 1.0 indicating complete co-occurrence. Since the intent in this analysis was descriptive rather than inferential as in Fager's case, his constraint that A at least equal half of B, or vice versa, was disregarded.

The composition of species groupings and relationships among these groupings were determined by using  $I_{AB}$  values for each species pair with a group-averaging method of classification to construct a dendrogram (Southwood 1966).  $\bar{I}_{AB}$  was used as the criterion for delimiting major assemblages.

Temporal stability was examined by comparing species composition in consecutive surveys. Consecutive species lists were compared by the Quotient of Similarity (QS), mathematically identical to  $I_{AB}$ , but with differing definition of terms, where:

$$QS = 2J/(A + B), \text{ and}$$

A = number of species in survey A,

B = number of species in survey B, and

C = number of species in common between the two surveys.

## Results

### *Species Composition*

More than 25 hydroid species were identified in the studies of Hueneme Shelf (Table 1). Fourteen species representing seven families were observed in association with soft substrate with sufficient frequency that they appear to constitute soft-bottom hydroid assemblages (Table 2). Some frequently observed species were not included in the soft-bottom assemblages because they are known also to occur commonly on algae, etc., in rocky areas throughout southern California (pers. obs.). These include: *Perigonimus ?repens*, frequently observed on shell debris; *Campanularia urceolata* and *Obelia* spp., all frequent epibionts on other hydroids, algae, and bryozoans; *Plumularia setacea*; and *Aglaophenia struthionides*, frequently found mixed in with populations of *Aglaophenia dispar*. *Clytia universitatis* also could have been excluded from this grouping in view of Torrey's reports on its occurrence on ferry docks and pilings but was included because of its high densities in soft-bottom habitats and its strong association with typically infaunal tubicolous polychaetes.

The hydroids comprising the soft-bottom hydroid assemblages can be segregated into several groups on the basis of general organization and size. Three species (viz., *Corymorpha palma*, *Euphysa* sp., and *Tubularia* sp. A) are solitary forms. These were observed at the deeper stations. The remaining species are colonial



Table 1. Hydroid species identified in studies on Hueneme Shelf.

| Athecata                                   | Thecata (continued)                        |
|--------------------------------------------|--------------------------------------------|
| Bougainvilliidae                           | Sertulariidae                              |
| Bougainvilliidae, unid. <sup>1</sup>       | <i>Hydrallmania distans</i>                |
| <i>Perigonimus ?repens</i>                 | <i>Sertularella pedrensis</i> <sup>2</sup> |
| Corymorphidae                              | <i>S. turgida</i> <sup>2</sup>             |
| <i>Corymorpha palma</i>                    | <i>Thuiaria ?alba</i>                      |
| <i>Euphysa</i> sp.                         | Plumulariidae                              |
| Tubulariidae                               | <i>Aglaophenia dispar</i>                  |
| <i>Tubularia</i> sp. A                     | <i>A. ?epizoica</i> <sup>4</sup>           |
| Thecata                                    | <i>A. ?fluxa</i> <sup>5</sup>              |
| Campanulariidae                            | <i>A. lophocarpa</i>                       |
| <i>Campanularia urceolata</i> <sup>2</sup> | <i>A. struthionides</i> <sup>2</sup>       |
| <i>Clytia bakeri</i>                       | <i>Plumularia alicia</i>                   |
| <i>Clytia universitatis</i>                | <i>P. mobilis</i>                          |
| <i>Obelia commissuralis</i> <sup>2</sup>   | <i>P. setacea</i> <sup>2</sup>             |
| <i>O. dichotoma</i> <sup>2</sup>           | Olindiidae                                 |
| <i>O. geniculata</i> <sup>2</sup>          | <i>Monobrachium parasitum</i>              |
| Campanulinidae                             |                                            |
| <i>Egmundella gracilis</i> <sup>3</sup>    |                                            |
| <i>Lovenella nodosa</i>                    |                                            |
| <i>Phialella ?rugosa</i>                   |                                            |

<sup>1</sup> Not included because of taxonomic problems.

<sup>2</sup> Found in other habitats.

<sup>3</sup> Too uncommon to determine association.

<sup>4</sup> Probably synonymous with *A. struthionides*.

<sup>5</sup> Probably synonymous with *A. dispar*.

forms. Most of the colonial species and two of the solitary species are macroscopic, growing to a length of at least several centimeters and with the capability of extending a few centimeters into the water over the sea floor to feed. In contrast, two microscopic species (the solitary *Euphysa* sp. and the colonial *Monobrachium parasitum*) never exceed a centimeter in length and are constrained to feed at the water-sand interface.

### General Quantitative Patterns

Patterns of bathymetric distribution and abundance are indicated in Table 2. Species richness was lowest at the shallower depths and highest at moderate depths. Peaks in density were observed at 15 to 24 m and at 45 to 60 m. With the exception of the 45- to 60-m zone, density decreased evenly on either side of the 15- to 24-m zone. The macroscopic species peaked in density at 15 to 24 m whereas the microscopic species were most abundant at 45 to 60 m.

### Composition and Distribution Patterns of Species Groups

An association matrix was compiled for the species in Table 2 based on the survey reports for Ormond Beach (IRC 1971; MBC, 1972a and b, 1973a and b, 1974a and b, and 1975; EQA and MBC 1974a, b, and c, and 1975a). Indices of affinity were calculated for each species pair and the group-averaging technique was used to construct a dendrogram indicating species relationships (Fig. 2). The mean degree of affinity between species pairs was  $0.14 \pm 0.19$ . This low level of

Table 2. Frequency of occurrence and average density (no./m<sup>2</sup>) by species and depth zone for hydroids on the Hueneme Shelf.

| Species                          | Depth of zone |                |      |       |       |       |       |                   |   | No. of times observed |  |
|----------------------------------|---------------|----------------|------|-------|-------|-------|-------|-------------------|---|-----------------------|--|
|                                  | 3-5           | 5-7            | 7-11 | 11-15 | 15-24 | 24-33 | 33-45 | 45-60             |   |                       |  |
| <i>Clytia bakeri</i> —%          | 60            | 20             | 0    | 20    | 0     | 0     | 0     | 0                 | 0 | 5                     |  |
| Highest density                  | 0.04          | — <sup>1</sup> | 0    | —     | 0     | 0     | 0     | 0                 | 0 |                       |  |
| <i>Phialella ?rugosa</i> —%      | 9             | 35             | 40   | 16    | 0     | 0     | 0     | 0                 | 0 | 43                    |  |
| Highest density                  | 0.7           | 0.14           | 0.79 | —     | 0     | 0     | 0     | 0                 | 0 |                       |  |
| <i>Clytia universitatis</i> —%   | 0             | 10             | 10   | 16    | 65    | 0     | 0     | 0                 | 0 | 16                    |  |
| Highest density                  | 0             | 0.07           | 0.14 | 1.93  | 0.40  | 0     | 0     | 0                 | 0 |                       |  |
| <i>Aglaophenia dispar</i> —%     | 0             | 4              | 11   | 22    | 29    | 27    | 8     | 0                 | 0 | 80                    |  |
| Highest density                  | 0             | 0.07           | 0.27 | 4.13  | 29.33 | 3.30  | 0.50  | 0                 | 0 |                       |  |
| <i>Lovenella nodosa</i> —%       | 0             | 0              | 7    | 93    | 0     | 0     | 0     | 0                 | 0 | 15                    |  |
| Highest density                  | 0             | 0              | —    | 0.07  | 0     | 0     | 0     | 0                 | 0 |                       |  |
| <i>Plumularia alicia</i> —%      | 0             | 0              | 5    | 29    | 51    | 15    | 0     | 0                 | 0 | 26                    |  |
| Highest density                  | 0             | 0              | 0.20 | 0.13  | 2.60  | 0.30  | 0     | 0                 | 0 |                       |  |
| <i>Hydrallmania distans</i> —%   | 0             | 0              | 8    | 26    | 40    | 26    | 0     | 0                 | 0 | 46                    |  |
| Highest density                  | 0             | 0              | 0.04 | 0.75  | 0.33  | —     | 0     | 0                 | 0 |                       |  |
| <i>Tubularia</i> sp. A—%         | 0             | 0              | 2    | 5     | 9     | 25    | 30    | 30                | 0 | 31                    |  |
| Highest density                  | 0             | 0              | 0.13 | 0.23  | 0.07  | 2.50  | 0.60  | 1.00              | 0 |                       |  |
| <i>Aglaophenia lophocarpa</i> —% | 0             | 0              | 0    | 8     | 38    | 31    | 0     | 23                | 0 | 13                    |  |
| Highest density                  | 0             | 0              | 0    | 0.01  | 0.07  | 0.40  | 0     | 0.60              | 0 |                       |  |
| <i>Euphysa</i> sp.—%             | 0             | 0              | 0    | 0     | 20    | 40    | 20    | 20                | 0 | 10                    |  |
| Highest density                  | 0             | 0              | 0    | 0     | 24.2  | 8.0   | 8.0   | 8.0               | 0 |                       |  |
| <i>Corymorpha palma</i> —%       | 0             | 0              | 0    | 0     | 0     | 100   | 0     | 0                 | 0 | 2                     |  |
| Highest density                  | 0             | 0              | 0    | 0     | 0     | 0.12  | 0     | 0                 | 0 |                       |  |
| <i>Thuiaria ?alba</i> —%         | 0             | 0              | 0    | 0     | 0     | 8     | 33    | 58                | 0 | 12                    |  |
| Highest density                  | 0             | 0              | 0    | 0     | 0     | 0.10  | 0.8   | 2.50              | 0 |                       |  |
| <i>Plumularia mobilis</i> —%     | 0             | 0              | 0    | 0     | 0     | 31    | 23    | 4.6               | 0 | 12                    |  |
| Highest density                  | 0             | 0              | 0    | 0     | 0     | 0.30  | 0.20  | 1.30              | 0 |                       |  |
| <i>Monobrachium parasitum</i> —% | 0             | 0              | 0    | 0     | 0     | 0     | 0     | 100               | 0 | 9                     |  |
| Highest density                  | 0             | 0              | 0    | 0     | 0     | 0     | 0     | 24.2 <sup>2</sup> | 0 |                       |  |

<sup>1</sup> — indicates inadequacy or absence of data.

<sup>2</sup> Minimum estimate; only presence was indicated in sampling data.



association indicates a high degree of heterogeneity and is consistent with the patterns indicated in Table 2.

A comparison of Table 2 and Fig. 2 indicates that the three major groups are segregated by depth-related factors. Members of the shallow-water species group (*Clytia bakeri* and *Phialella ?rugosa*) have a low level of affinity between themselves and virtually none to the other species groups. The mid-depth group, predominated by *Aglaophenia dispar* and *Hydrallmania distans*, has a moderate degree of affinity, but has little with the other groups. The two sub-groups that comprise the deep-water group are also segregated by depth-related factors. One of these sub-groups includes mainly species that extend into deeper water (*Plumularia mobilis*, *Monobrachium parasitum*, and *Thuiaria ?alba*), whereas the other sub-group includes species characteristic of moderate depths (*Corymorpha palma* and *Aglaophenia lophocarpa*).

### *Temporal Stability*

Temporal stability of the hydroid assemblage was examined by assessing similarity in species composition between consecutive surveys (Table 3). This analysis indicates a strong temporal similarity between consecutive surveys within the Ormond Beach and Oxnard data sets ( $\bar{x} \pm s = 0.68 \pm 0.16$ ). Considering that consecutive surveys often represent seasonal opposition and, in the case of the Oxnard survey, different sampling techniques, this seems quite a high level of stability.

## Discussion

### *Factors Controlling Distribution*

Surge activity appears to be a major factor controlling the distribution of the hydroid species on the Hueneme Shelf, as Oliver et al. (1980) described for benthic invertebrate assemblages in Monterey Bay. In addition to its direct physical effects in shallow water, surge probably operates indirectly through its influence on other important factors. Substrate availability is affected through the influence of surge activity on the distribution of many species used for substrate (e.g., bean and Pismo clams, sand dollars, and tubicolous polychaetes). Surge activity correlates inversely with stability of the sediment but directly with sediment disturbance (Shepard 1963) and the concentration of suspended food particles (Jorgensen 1966).

*Corymorpha*, *Euphysa*, and *Monobrachium* live in intimate association with the substrate but are poorly protected from abrasion. Furthermore, the first two species require relatively undisturbed sediment for effective anchoring, and probably do not re-establish readily if "uprooted." These characteristics preclude successful recruitment to areas where surge activity routinely disturbs the substrate and resuspends sediments.

With the exception of the corymorphid species, all of the hydroids in this area have a morphological requirement for a hard or stable substrate upon which to settle and grow. In fact, a variety of hard substrates is available on soft bottom of the Hueneme Shelf, but relative abundance is low (personal observation). Potentially suitable substrates in the study area included shells of living and dead mollusks, sand-dollar tests, worm tubes, crab carapaces, and algae. The availability

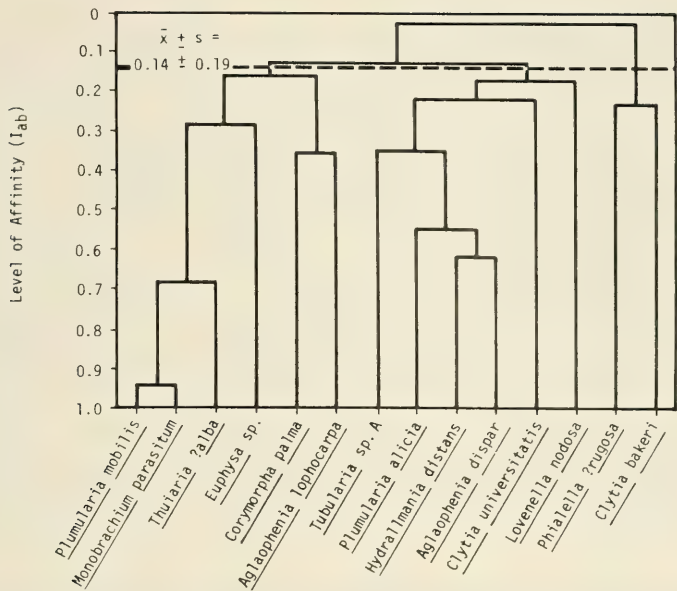


Fig. 2. Dendrogram showing relationships among dominant soft-bottom hydroids on the Hueneme Shelf, based on distribution patterns.

of suitable substrate may become limiting at times. However, the probability of significant intra- or inter-specific competition for substrate on the Hueneme shelf appears low based on the low density of hydroids relative to that of some available substrate (Table 4).

Most of the hydroid species found in the study area were growing on worm tubes. These structures provide a moderate degree of substrate diversity for epibionts. Tubicolous polychaetes were generally dominant macrofaunal forms from depths of 10 to 60 m (Table 4). Twenty species of tubicolous polychaete were large enough for diver identification. Hydroid colonies inhabited at least five common types of tube. These included:

- (1) Stiff, coarse parchment-like tubes incorporating shell debris and/or algae (e.g., *Diopatra ornata* and *D. splendidissima*).
- (2) Fine, flexible parchment-like tubes incorporating shell debris (e.g., *Loimia medusa* and *Ampharete labrops*).
- (3) Flexible parchment-like tubes incorporating a surface layer of sand (e.g., *Mesochaetopterus rickettsii*, *Onuphis* spp., and *Nothria* spp.).
- (4) Flexible parchment-like tubes without inclusions (e.g., *Pista* spp. and *Eudistylia vancouveri*).
- (5) Brittle sand tubes (e.g., *Axiothella* spp.).

A sixth tube type, typified by *Diopatra tridentata*, reaches only to the sand-water interface and did not appear to support epibionts.

Type 1 tubes appeared to be the overwhelming favorite of most epibionts, including hydroids (pers. obs.). Type 1 tubes generally have several characteristics that may be responsible for this apparent preference. They often belong to perennial worms. They are sufficiently tough and resilient to withstand the added



Table 3. Relative frequency of occurrence among stations for selected hydroids observed in surveys on the Hueneme Shelf.

| Species                                    | OBM<br>10/71 | OBM<br>4/72 | OBM<br>8/72 | OBM<br>1/73 | OBM<br>7-8/73     | Oxnard<br>12/73 | OBM<br>1/74       | Oxnard<br>3/74 | Oxnard<br>6/74    | OBM<br>8/74       | Oxnard<br>11/74 | OBM<br>2/75 |
|--------------------------------------------|--------------|-------------|-------------|-------------|-------------------|-----------------|-------------------|----------------|-------------------|-------------------|-----------------|-------------|
| <i>Clytia bakeri</i>                       |              |             |             |             | 0.07              |                 | 0.13 <sup>2</sup> |                |                   | 0.06              |                 | 0.06        |
| <i>Phialella ?rugosa</i>                   | 0.20         | 0.15        | 0.15        | 0.25        | 0.31 <sup>2</sup> |                 | 0.02              |                |                   | 0.31 <sup>2</sup> |                 | 0.75        |
| <i>Clytia universitatis</i>                |              | 0.05        |             | 0.45        |                   | 0.05            |                   |                |                   |                   | 0.17            |             |
| <i>Aglaophenia dispar</i>                  | 0.20         | 0.35        | 0.35        | 0.15        | 0.13              | 0.05            | 0.29              | 0.71           | 0.32              | 0.13              | 0.42            | 0.13        |
| <i>Tubularia</i> sp. A                     | 0.05         | 0.15        |             |             |                   | 0.11            | 0.07              | 0.42           |                   |                   | 0.50            |             |
| <i>Lovenella nodosa</i>                    |              | 0.10        | 0.10        | 0.20        | 0.07 <sup>2</sup> |                 | 0.04 <sup>2</sup> | 0.04           |                   |                   |                 | 0.06        |
| <i>Hydrallmania distans</i>                | 0.15         | 0.35        | 0.25        | 0.25        | 0.04              |                 | 0.18              | 0.33           |                   |                   | 0.25            | 0.06        |
| <i>Plumularia alicia</i>                   | 0.05         | 0.20        |             | 0.05        | 0.13              | 0.11            |                   | 0.25           |                   | 0.06              | 0.25            | 0.06        |
| <i>Aglaophenia lophocarpa</i> <sup>3</sup> |              |             |             |             |                   | 0.11            |                   | 0.08           | 0.11              |                   | 0.29            |             |
| <i>Euphyssa</i> sp. <sup>3</sup>           |              |             |             |             |                   | 0.11            |                   | 0.21           | 0.16 <sup>2</sup> |                   | 0.08            |             |
| <i>Corymorpha palma</i> <sup>3</sup>       |              |             |             |             |                   |                 |                   | 0.25           |                   |                   | 0.25            |             |
| <i>Thuiaria ?alba</i> <sup>3</sup>         |              |             |             |             |                   |                 |                   | 0.04           |                   |                   | 0.21            |             |
| <i>Plumularia mobilis</i> <sup>3</sup>     |              |             |             |             |                   | 0.05            |                   | 0.17           | 0.16              |                   |                 |             |
| <i>Monobrachium parasitum</i> <sup>3</sup> |              |             |             |             |                   | 0.11            |                   |                |                   |                   |                 |             |
| Type of survey(s) <sup>1</sup>             | D & I        | D & I       | D & I       | D & I       | D & I             | I               | D & I             | D, I & S       | I                 | D & I             | D, I & S        | D & I       |
| Depth range (m)                            | 3-12         | 3-12        | 3-12        | 3-12        | 3-12              | 9-55            | 3-12              | 9-55           | 9-55              | 3-12              | 9-55            | 3-12        |
| Number of stations                         | 20           | 20          | 20          | 20          | 45                | 19              | 45                | 24             | 19                | 16                | 24              | 16          |

<sup>1</sup> D = diver observation; I = infaunal samples; S = submersible observations.<sup>2</sup> Reproductively mature.<sup>3</sup> Species only found at greater than 12.2-m depths in the study area.

Table 4. Number of species and density for hydroids and tubicolous polychaetes at various depths on the Hueneme Shelf.

| Depth<br>(m) | Hydroids                        |                               | Tubicolous polychaetes          |                               | Dominant polychaete species                             |
|--------------|---------------------------------|-------------------------------|---------------------------------|-------------------------------|---------------------------------------------------------|
|              | Average<br>number of<br>species | Average<br>density<br>(no./m) | Average<br>number of<br>species | Average<br>density<br>(no./m) |                                                         |
| 6            | 0.6 ± 0.8                       | 0.02 ± 0.04                   | 2.6 ± 1.7                       | 0.7 ± 0.7                     | <i>Diopatra splendidissima</i>                          |
| 9            | 0.5 ± 0.6                       | 0.08 ± 0.12                   | 4.0 ± 2.5                       | 1.3 ± 1.7                     | <i>D. splendidissima</i> and <i>D. ornata</i>           |
| 12           | 2.8 ± 1.0                       | 0.6 ± 0.3                     | 6.8 ± 2.0                       | 2.4 ± 1.2                     | <i>D. ornata</i>                                        |
| 14           | 1.8 ± 1.5                       | 1.3 ± 1.4                     | 6.9 ± 3.1                       | 28.0 ± 61.6                   | <i>D. ornata</i> and <i>Nothria</i> spp.                |
| 18           | 3.1 ± 1.5                       | 9.6 ± 15.0                    | 6.1 ± 1.6                       | 97.9 ± 30.1                   | <i>D. ornata</i> and <i>Nothria</i> spp.                |
| 28           | 3.8 ± 1.5                       | 1.7 ± 1.0                     | 4.6 ± 2.1                       | 1.8 ± 1.3                     | None                                                    |
| 37           | 2.7 ± 1.0                       | 0.7 ± 0.4                     | 4.0 ± 1.8                       | 23.6 ± 31.1                   | <i>Lanice conchilega</i> and <i>Praxillura maculata</i> |
| 55           | 2.8 ± 1.4                       | 1.7 ± 1.3                     | 4.6 ± 1.9                       | 22.0 ± 26.9                   | <i>Lanice conchilega</i> and <i>Praxillura maculata</i> |

<sup>1</sup> Based on studies for So. Calif. Edison Co. and the Oxnard Sanitation District by MBC.

drag attendant to attached epibionts and extend at least a few centimeters above the abrasive sand-water interface. They usually occur in areas of considerable water movement and nutrient resuspension. Finally, they provide a stable or "stony" surface upon which epibionts can settle and grow. Tubes of Type 2 through 5 generally lack at least one of these characteristics, resulting in lower suitability to epibionts.

Despite the general availability of worm tubes across the depth gradient, the depth ranges of the various hydroid species associated with worm tubes exhibited strong bathymetric zonation patterns (Table 2). Furthermore, the polychaetes exhibited strong depth patterns that apparently affected the quality of potential substrate available to the hydroids. Generally, Type 1 tubes were restricted to portions of the study area from 6 to 25 m deep (EQA and MBC 1974b and 1975a), but the most frequently colonized species (*Diopatra ornata*) was most common from 15 to 25 m (Table 4). For more than one-third of the hydroid species, frequency of occurrence and maximum density peaked in this depth zone. It is notable that highest species richness and densities (Table 2) and the larger species of epifaunal hydroids occurred in this depth range. In contrast, both tubicolous polychaetes and hydroids using tubes for settlement suffered attrition in the 6- to 9-m depth range from the constant grinding of the dense sand-dollar populations (pers. obs.).

Below 27 m, the dominant polychaetes did not appear to support many hydroid species. In this area, it seems that wave action is generally ineffective at resuspending organic detritus and winnowing out fine sediments. As a consequence, deposit-feeding assemblages dominated by the echiurid *Listriolobus pelodes* replace the suspension feeders of the upper levels of the shelf (EQA and MBC 1974b and 1975a). *Praxillura* and possibly *Lanice*, although suspension feeders, capture food on a slightly inverted "umbrella" of mucus that is spread on the tessellations or "spokes" surrounding the tube aperture (McDaniel and Banse 1979, pers. obs.). This delicate mode of feeding is mainly effective only in mild currents and with fine food particles; it also may effectively combat "fouling" by epibionts because



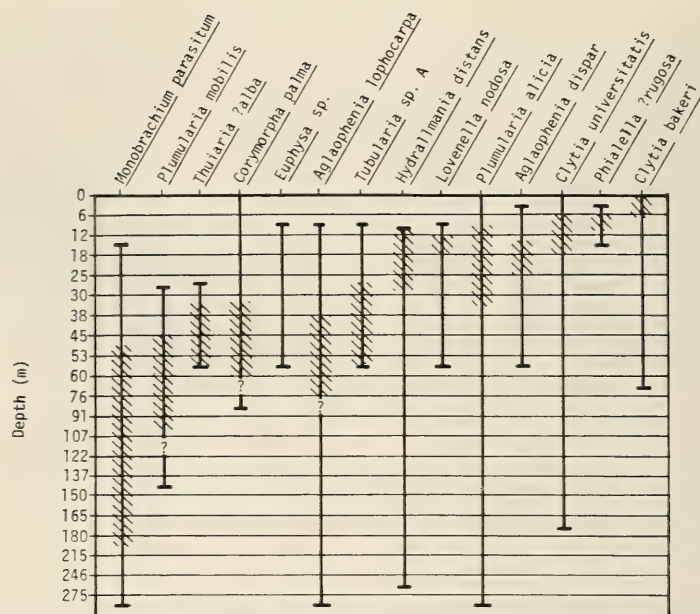


Fig. 3. Bathymetric ranges (—) reported for species in the Hueneme Shelf hydroid assemblage and their zones of dominance (////) in the study area. Listing order corresponds to depth relationships.

it captures the settling larvae. Also, the probable relative paucity of suspended prey species and organic detritus in this quiescent environment may limit hydroid success.

Shell material is also an important substrate for several local hydroid species, as noted by previous authors (e.g., Fraser 1912; Naumov 1960). *Clytia bakeri* is strongly associated with Pismo clams (*Tivela stultorum*) and bean clams (*Donax gouldii*) (Torrey 1904). The depth ranges of these clams (Fitch 1950; Ricketts and Calvin 1968) overlap substantially with the zone of dominance of *C. bakeri*. *Phialella ?rugosa* and *Lovenella nodosa* were observed primarily on fragments of sand-dollar tests and were generally restricted to the depth range of sand-dollar beds. *Monobrachium parasitum* was observed only at the deepest stations (55 m) on the clam *Axinopsida serricata*. As *Axinopsida* was also seen at all 36-m stations and half of those at 27 m, the upper limits of *Monobrachium* must be imposed by some factor other than substrate.

Another factor of undoubtedly great importance in determining the distribution of hydroids is food availability. Hyman (1940) states that hydroids are "chiefly carnivorous, ingesting any small animal of appropriate size that happens to come in contact with the tentacles." However, in addition to small live animals such as larvae, crustaceans, nematodes and other worms, "newly dead animals or portions thereof are also ingested." She further discusses several experiments in which hydroids were induced to ingest bits of sponge, gelatin, or fibrin soaked in animal juices, and suggests that at least some species may be less selective than previously suspected. Hydroids may supplement their animal diet with resuspended particles of organic detritus and associated bacteria, much in the same fashion as many of the suspension-feeding polychaetes that characterize the in-

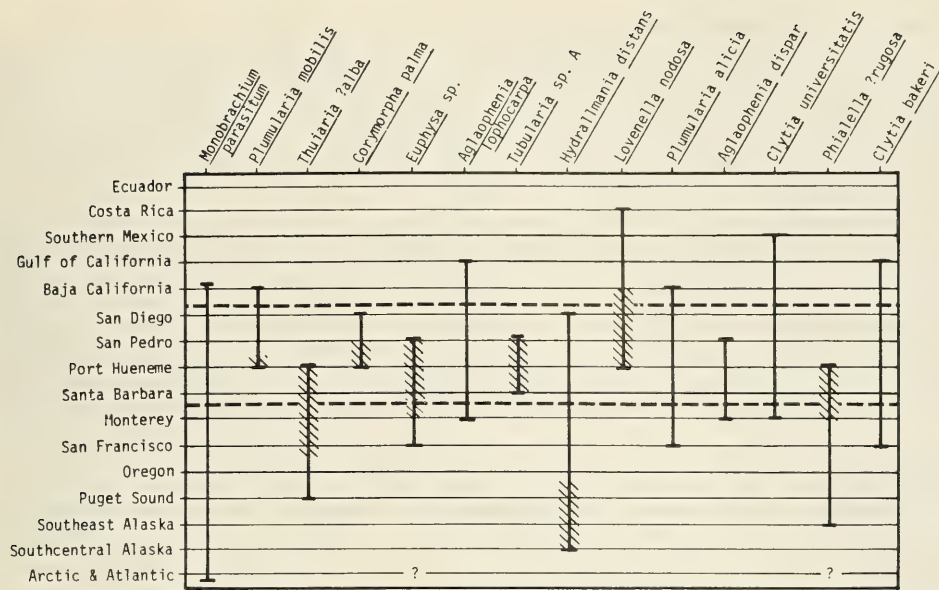


Fig. 4. Reported geographic distributions (|—|) and range extensions (/////|) for species in the Hueneme Shelf hydroid assemblage. Listing order corresponds to depth relationships.

intermediate depths of this study area. *Corymorpha* is reported to bend over in order to place the mouth and tentacles in contact with the bottom sediments and has obviously adapted to take advantage of the rich source of protein found in the bacteria associated with detritus on soft substrates (Jorgensen 1966). Other hydroids, particularly such forms as *Euphyssa* and *Monobrachium*, also may take advantage of the organic detritus in suspension near the bottom, as well as the numerous small crustaceans and worms that occur in the water near the water-sand interface.

Patterns in Distribution

Despite the strong tendency for these hydroid species to occur in areas of soft substrate, the data in Table 2 do not suggest strong positive interactions among the species. Correlations in depth distribution patterns among the species appear weak. Instead, the assemblage described for any particular depth zone (Table 2) or by analytical techniques (Fig. 2) seems to reflect the summation of independent depth ranges (Fig. 3). Furthermore, a comparison of the known geographic ranges of these species suggests that they do not form integral units on a geographic basis (Fig. 4). The hydroid assemblage on the Hueneme Shelf includes representatives of both southern and northern faunas, and two species are apparently endemic to the southern California Bight. Five species have ranges extending both north and south of southern California. Three species (*Clytia bakeri*, *C. universitatis*, and *Lovenella nodosa*) co-occurred in several dredge hauls as far south as Chachahua Bay, Mexico (Fraser 1938c, 1948), but in most other collections each inhabited a distinct depth range or substrate. Thus, it appears likely that the observed assemblages are a consequence of chance association rather than of interspecific interactions.



*Notes on the Natural History of the Shelf Hydroids*

In the course of this study, a considerable amount of published and unpublished information on the species inhabiting the Hueneme Shelf has become available. These data are summarized and synthesized by species in the following section in an attempt to provide preliminary descriptions of their respective niches and natural history.

*Corymorpha palma* Torrey 1902: This species apparently has a very restricted geographic range. Since it was described from San Pedro Bay, its known range had only been expanded to include San Diego Bay (Torrey 1902, 1904) and Newport Bay (Ricketts and Calvin 1968). It has been reported primarily from intertidal habitats. The only previous reports from subtidal habitats were from 21 m on fine sediments off Hermosa Beach (Turner et al. 1969) and from up to 5 m in Newport Bay (Ball 1973). Subtidal populations were observed at Isthmus Cove, Santa Catalina Island (8 m deep, gently sloping mud bottom, March 1967), near a shipyard in San Diego Bay (6 m deep, mud bottom, June 1974), and at low densities at two locations on the Hueneme Shelf (27 m deep, on silty sand, November 1974; Tables 2 and 3). Moreover, in January 1975, three specimens clearly ascribable to *C. palma* were collected by divers from a mud bottom at a depth of 85 m in Santa Monica Bay, near the Hyperion outfall of the Los Angeles City Sanitation District. Thus, *C. palma* is now known to occur on mud substrates from Port Hueneme to San Diego and from the low intertidal zone out to at least 85 m.

Torrey (1902) reported that *C. palma* is large (up to 15 cm long) and occurs anchored by filamentous processes in the substrate on intertidal sand and mud flats throughout the year. In 1904, he reported the occurrence of "eggs" in May, June, and July. The specimens collected subtidally in March 1967 and January 1975 supported nearly mature medusa buds. Thus, it appears that the species may reproduce at least in winter, spring, and summer.

*Euphysa* sp.: This tiny, solitary species was observed at low densities in infaunal samples from fine sediments at depths of 23 m or more on the Hueneme Shelf, and inside Redondo Harbor, a shallow, protected boat harbor. Frequency of occurrence in the study area was highest in March 1974. Specimens collected in January and June were becoming reproductively mature.

The specimens collected agree with Russell's (1953) description of *Euphysa aurata*, except that (1) the loosely fitting perisarc is rather funnel-shaped at its distal end to accommodate the lower portion of the hydranth, and (2) the anchor filaments often are numerous and create a small mass of sand. The upper (larger) portion of the perisarc is moderately wrinkled and gray-brown in color. Total length ranged from 0.2 to 1.2 cm, the capitate oral tentacles numbered from 3 to 6, and the moniliform proximal tentacles numbered from 7 to 12. On all specimens, 6 to 12 tubercles (possibly rudiments of anchor filaments; Rees 1957) were located on the proximal portion of the hydranth near the upper margin of the perisarc.

Species determination was not possible during this study since all specimens observed had been preserved, precluding the necessary culture of the medusae. The genus has been reported previously from the eastern Pacific by Jones (1961; San Francisco Bay, California).

*Tubularia* sp. A: This large (up to 15 cm long), apparently undescribed, species is fairly common on soft-bottom habitats along the coast of California from at least Montecito to Huntington Beach. It was observed growing singly on the tubes of polychaete worms, particularly *Diopatra ornata*. Its fragility is probably one reason it is undescribed; the large hydranth remained intact only on specimens which were hand-collected by divers. Key features include its large size, the solitary, unbranched growth form, the small number of proximal tentacles, and the ratio of oral to proximal tentacles. Its occurrence on polychaete tubes in soft-bottom habitats is uncommon for the genus.

*Tubularia* sp. A has been seen in January, March, April, September, October (Table 3), and December (pers. obs., Montecito, California, 11 m), but it was not observed at shallower stations in summer surveys. Also, it was not observed between April 1972 and January 1974 in the Ormond Beach study, suggesting long-term cycles (Table 3).

*Tubularia* sp. A was the fourth most commonly observed and abundant species on the Hueneme Shelf. Its bathymetric range, extending from 7 m to at least 60 m (Table 2), was the broadest observed. Most specimens were encountered at depths of 27 m or more.

*Clytia bakeri* Torrey 1904: This robust species was observed only infrequently in these studies, mainly at stations less than 4 m deep (Table 2). Torrey (1904) described it from dense intertidal populations. It lives attached to the shells of the bean clam *Donax gouldii* (Torrey 1904), the Pismo clam *Tivela stultorum* (Fraser 1937; Fitch 1950), and the tests of the sand dollar *Dendraster excentricus* (Merrill and Hobson 1970; pers. obs.). Its geographic range extends from San Francisco, California, to Chacahua Bay, Mexico, where it was dredged in 9 to 18 fathoms (Fraser 1938c). It has been collected from 71 m (Fraser 1937), but occurrences at depths greater than 10 m are probably exceptional.

*Clytia universitatis* Torrey 1904: This large, bushy, fascicled species occurred most frequently from 11 to 15 m (Table 2) where densities were also highest. Most specimens were attached to worm tubes, particularly those of *Diopatra ornata*. The species was described from specimens collected intertidally on wharf pilings or floats in San Diego and San Pedro bays, California. Subsequently, it has been reported frequently from San Francisco Bay, California, (Fraser 1937) to Port Parker, Costa Rica, and to depths of 183 m (Fraser 1948).

Populations of *C. universitatis* exhibit a strong seasonal component. During the 1971–1972 thermal effects studies for power plants in southern California, I observed a “bloom” of *C. universitatis* near Long Beach. Densities exceeded 100 colonies/m<sup>2</sup> in areas where densities of the “host” worm tubes approached 200/m<sup>2</sup>. These high densities and the large colony size occasionally combine to add considerably to the bottom relief on flat, soft-sediment habitats.

Records from both the Ormond Beach and Oxnard surveys indicate that it occurs most frequently during winter months and infrequently during the summer (Table 3). My records from Santa Catalina Island indicate a similar pattern.

*Lovenella nodosa* Fraser 1938: This graceful species was observed infrequently by divers from 7 to 15 m (Table 2) on fragments of shell and sand-dollar tests. The previously recorded range was from Thurloe Point, Baja California, south to Cape San Francisco, Ecuador, at depths from 9 to 55 m (Fraser 1938a, c, and



1948). Its discovery on the Hueneme Shelf constitutes a substantial range extension. Observations have been concentrated from 11 to 18 m.

Despite its apparent southern origins, *L. nodosa* occurred throughout the year and was observed in reproductive condition both in mid-winter and mid-summer (Table 3).

*Phialella ?rugosa* (Nutting 1901): This inconspicuous species was the most frequently observed hydroid in these studies (Table 2). It was observed in infaunal samples and by divers in all seasons and was reproductively mature during summer and winter (Table 3). All observations were at depths of less than 15 m with greatest abundance from 4 to 11 m, a depth dominated by the sand dollar *Dendraster excentricus*. *Phialella ?rugosa* occurred most frequently on fragments of sand-dollar test, although occasionally it was observed attached to the tube of the polychaete *Diopatra splendidissima*, also common in this depth zone. Nutting (1901) reported that the type specimen was growing on another hydroid (*Obelia* sp.).

The specimens observed on the Hueneme Shelf have been tentatively assigned to *P. rugosa* (Nutting 1901), previously reported to occur from Juneau, Alaska, to Oakland, California. However, because of the similarity of *P. rugosa* and *P. quadrata* (see Russell 1953) and the absence of information on the medusa of the local species, this identification is queried.

*Hydrallmania distans* Nutting 1899: This species, distinctive due to its gracefully paniced branching, was the second most frequently observed hydroid in these studies, although at least six other macrofaunal hydroids occurred in higher densities (Table 2). It was observed in all seasons and nearly all surveys (Table 3) growing on polychaete worm tubes from 7 to 33 m. Highest densities were recorded from 10 to 15 m (Table 2).

*Hydrallmania distans* has been previously recorded from the Queen Charlotte Islands, British Columbia, to Coronado Beach, California, across a depth range from 5 to 275 m (Fraser 1937 and 1948). Generally, shallower records (11–26 m) predominated. (In other studies, I have observed *H. distans* in lower Cook Inlet, Alaska. Specimens were collected toward the eastern end of Kachemak Bay, on muddy-cobble and shell-hash substrate in about 27 m, and at Black Reef, in Kamishak Bay, in a silty boulder field at a depth of about 7 m. Specimens collected in June 1978 were reproductively mature.)

*Thuiaria ?alba* Fraser 1911: Distinguished by its silvery plumose appearance, this hydroid was encountered in moderate densities on polychaete worm tubes at the deeper stations (Table 2). Both frequency of occurrence and density were highest at the deepest level studied. The species was observed during both March and November (EQA and MBC 1974b and 1975a).

*Aglaophenia dispar* Fraser 1948: This conspicuous, bushy species was observed most frequently (all surveys) and was the most abundant hydroid species in the study area (Tables 2 and 3) as well as generally on soft-bottom substrates in southern California (pers. obs.). Both frequency of occurrence and density peaked at from 15 to 25 m (Table 2). I have observed it at densities exceeding 100 colonies/m<sup>2</sup> off Los Alamitos, California, usually attached to large tubes of worms such as *Diopatra ornata*, *Loimia medusa*, or *Pista* spp. Its density was closely related to the density of polychaetes with large, tough, flexible tubes. Its bathymetric range was among the broadest of the hydroids in the soft-bottom assem-

blages. This highly variable, branching species has been reported from Monterey Bay to Huntington Beach, California, from 5 to 57 m (Fraser 1948).

*Aglaophenia lophocarpa* Allman 1877: This species was infrequently observed at moderate densities on worm tubes from depths of 10 to 60 m (Table 2). It occurred in all seasons (Table 3). Frequency of occurrence was highest from 15 to 33 m but density was greatest from 45 to 60 m. Its absence in observations between 33 and 45 m is probably a sampling artifact.

It has previously been recorded from Pacific Grove, California, to San Pedro Nolasco Island, Baja California. It appears to inhabit mainly deeper areas, having been found at depths ranging from 9 to 440 m, with only two of eight previous observations at depths less than 36 m (Fraser 1938b and 1948).

*Plumularia alicia* Torrey 1902: This species was observed at moderate densities from 7 to 33 m (Table 2) growing mainly on tubes of worms such as *Diopatra ornata*. It was observed most frequently and at highest densities from 15 to 24 m. It occurred in all seasons (Table 3).

Its recorded geographic range extends from Heceta Head, Oregon, to Cedros Island, Baja California (Fraser 1937 and 1938a). The reported bathymetric range extends from the intertidal zone to 330 m but most observations have been less than 37 m. Torrey (1902) reported collecting *P. alicia* from both sand and rock substrates.

*Plumularia mobilis* Fraser 1948: This small species was commonly seen in moderate densities only at the deeper stations in the study area (Table 2), also growing mainly on worm tubes. It was observed in March, November, and December (Table 3).

Fraser (1948) reported its range from Cedros Island, Baja California, from 82 to 148 m.

*Monobrachium parasitum* Mereschowsky 1877: This symbiotic species was observed at moderate densities in infaunal samples from the deepest stations (Table 2) living on shells of small live bivalves, mainly *Axinopsida serricata*. As with *Euphysa* sp., it was only detected during microscopic examination. It was observed in spring, summer, and winter (Table 3).

It has been reported frequently from the Arctic Ocean (Naumov 1960). It has also been reported in the eastern Pacific Ocean by Fraser (1937; British Columbia) and Hand (1957; Santa Monica Bay, California, and Todo Santos Bay, Baja California, Mexico). The bathymetric range extends from 8 to 308 m but most observations have been between 50 and 200 m.

After summarizing the published literature on *Monobrachium*, Hand (1957) reported that this hydroid previously had been found mainly on shells of living clams that lie very near the sediment surface in fine sand or soft silt. He observed only one specimen living otherwise, i.e., on an arenaceous foraminiferan.

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## Research Notes

### A Sublittoral Population of *Pleurophycus gardneri* Setchell and Saunders 1900 (Phaeophyceae: Laminariaceae) in Central California

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Published distributional records for the stipitate kelp *Pleurophycus gardneri* Setchell and Saunders 1900 (Phaeophyceae: Laminariaceae) indicate a geographic range from Montague Island (59°58'N, 147°22'W), Alaska to Fort Bragg (39°27'N, 123°47'W), California (Druehl 1969, 1970; Kjeldsen 1972). *P. gardneri* is found primarily in rocky intertidal and shallow subtidal locations (Scagel 1967; Nicholson 1976). In California, populations of *P. gardneri* have been reported only from the lower rocky intertidal near Fort Bragg (Kjeldsen 1972).

On 7 and 8 July 1982 and 23 March 1984 we censused stipitate kelps during SCUBA dives at a site 2.3 km south southeast of Pt. Sierra Nevada (35°41'N, 121°18'W). We counted kelps in 1 × 5-m plots along a 50-m tape laid across the bottom in an arbitrarily predetermined direction from the skiff anchor. We also measured water depth at 1-m intervals along the tape, using a SCUBA depth gauge. Depths were subsequently corrected to mean lower low water, using tide tables. On 20 August 1982, we used the same techniques to sample kelp densities at a site 2.4 km east southeast of Pt. Piedras Blancas (35°39'N, 121°15'W).

The most abundant kelps at the Pt. Sierra Nevada site were *Pterygophora californica* Ruprecht 1852 (Phaeophyceae: Alariaceae) and a species we tentatively identified as *P. gardneri* (Table 1). Based on specimens collected on 8 July 1982, our field identification was subsequently confirmed by I. A. Abbott. Voucher specimens were placed in the Gilbert M. Smith Herbarium at Hopkins Marine Station, Stanford University, Pacific Grove, California.

During July 1982, *P. gardneri* at the Pt. Sierra Nevada site ranged in length from 20 to 90 cm. All size classes within this range were well represented, and all plants appeared healthy. Densities of *P. gardneri* were low ( $<1.0/\text{m}^2$ ) at depths less than 16 m, but highly variable at greater depths (0–10.0/ $\text{m}^2$ ).

We could not relocate precisely the July 1982 site when we sampled the Pt. Sierra Nevada site in March 1984. However, we encountered a large stand of *P. gardneri* at a nearby site. Plants ranged in height from 22 to 83 cm. Highest densities (to 9.8/ $\text{m}^2$ ) again occurred at depths greater than 16 m. *P. californica* was extraordinarily abundant in the area (to 200.0/ $\text{m}^2$ ), a probable consequence of heavy recruitment which followed the severe storms of winter 1982–83 (VanBlaricom, unpub. data).

We located a single *P. gardneri* at the Pt. Piedras Blancas site in August 1982. The plant was 70 cm in length, attached to solid rock in 18.3 m of water, and appeared healthy. *P. californica* was the most abundant kelp in the area sampled (Table 1). This sighting constitutes the southernmost known limit of the geographic range of *P. gardneri*, 480 km southeast of the previously-reported southern limit.

Sporangial thalli of *P. gardneri* are described as "probably annual" (Fritsch 1945; Nicholson 1976). However, the condition of blades of *P. gardneri* observed

Table 1. Site descriptions and kelp densities, northern San Luis Obispo County, July–August 1982 and March 1984.

|                                                                                                                                       | Pt. Sierra Nevada                                  |                            | Pt. Piedras Blancas                            |
|---------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------|----------------------------|------------------------------------------------|
|                                                                                                                                       | July 1982                                          | March 1984                 | August 1982                                    |
| Depth range along transect (m)                                                                                                        | 14.0–17.4                                          | 13.5–17.4                  | 16.8–19.2                                      |
| Surface canopy type                                                                                                                   | <i>Nereocystis luetkeana</i>                       | None                       | <i>Macrocystis pyrifera</i>                    |
| Bottom type                                                                                                                           | Solid rock with small patches of gravel and cobble | Solid rock                 | Solid rock reefs separated by channels of sand |
| Maximum vertical relief (m)                                                                                                           | 1.5                                                | 2.7 (10-m pinnacle nearby) | 2.4 (7.6-m pinnacle nearby)                    |
| Kelp densities (mean number per m <sup>2</sup> [range]). Sample sizes (1 × 5-m plots): July 1982: 17; March 1984: 10; August 1982: 20 |                                                    |                            |                                                |
| <i>Pterygophora californica</i>                                                                                                       | 5.1 (1.6–12.0)                                     | 44.0 (0.2–200.0)           | 1.8 (0–6.6)                                    |
| <i>Pleurophycus gardneri</i>                                                                                                          | 3.2 (0–10.0)                                       | 1.5 (0–9.8)                | 0.01 (0–0.1)                                   |
| <i>Nereocystis luetkeana</i>                                                                                                          | 0.3 (0–3.4)                                        | 0                          | 0                                              |
| <i>Laminaria setchellii</i>                                                                                                           | 0.1 (0–0.4)                                        | 0.2 (0–0.8)                | 0.2 (0–0.8)                                    |
| <i>Macrocystis pyrifera</i>                                                                                                           | 0                                                  | 0                          | 0.1 (0–0.8)                                    |

in March 1984 indicated that many individuals may have survived through the previous winter. Distal portions of blades were dark brown and leathery, with tattered margins. Proximal portions were light brown and elastic, with margins entire. The two portions of blade were separated by sharply-defined discontinuities in color and texture. We interpreted this pattern to be new spring growth added to blade tissue produced during the previous growing season. Such patterns are common in other kelps in the area which produce blade tissue seasonally and are known to be perennial (e.g., *Laminaria setchellii* Silva 1957 [Phaeophyceae: Laminariaceae] and *P. californica*; VanBlaricom, unpub. data). These patterns have been described as characteristic of perennial species within the Laminariaceae (Setchell 1902; Fritsch 1945). Thus, we suggest that some *P. gardneri* at the Pt. Sierra Nevada site are perennial. Similar evidence indicates the possibility that intertidal populations on the coasts of Washington (state) and southeastern Alaska also include perennial individuals (P. K. Dayton, pers. comm.).

During 1977 through 1984 we made over 1000 research SCUBA dives in kelp forests between Pt. San Simeon (35°38'N, 121°12'W) and Ragged Pt. (35°46'N, 121°19'W), northern San Luis Obispo County, primarily at depths less than 15 m. We made no sightings of *P. gardneri* other than those reported here. Similarly, we have studied plant and animal communities in rocky intertidal habitats of the area since 1977 without once recording the presence of *P. gardneri*. We suggest that *P. gardneri* occurs primarily in isolated populations at depths exceeding 15 m in northern San Luis Obispo County. There has been little phytogeographic study of sublittoral rocky habitats in California north of our study area, except for areas near the Monterey Peninsula and Santa Cruz County (e.g., Murray et al. 1980). Therefore, we are unable to determine if our data are typical of the



distribution of *P. gardneri* in the southern part of its range. We note, however, that other kelps (e.g., *Eisenia arborea* Areschoug 1876 [Phaeophyceae: Alariaceae] and *Agarum fimbriatum* Harvey 1862 [Phaeophyceae: Laminariaceae]) apparently have strikingly disjunct distributions in the northeast Pacific (Druehl 1970; Nicholson 1976). A comparably disjunct pattern could account for the apparent rarity of *P. gardneri* in California.

On 23 August 1985 we made several research dives in dense forests of *Macrocystis pyrifera* at sites 4 km south southeast of Pt. Sur (36° 17'N, 121° 53'W) California, working from the research vessel *Westwind*. On departure from the site, we recovered two *Pleurophycus gardneri* entangled by the vessel anchor, retrieved from a depth of 27 m in a location seaward of the *Macrocystis* canopy. The plants were 100–120 cm in total length and appeared healthy and fresh. One plant had a patch of apparently fertile sori in the midrib. Thus, we suggest that a population of *P. gardneri* is present in the vicinity.

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## ***A Priori* Estimation of Sample Size and Number of Variables for Principal Components Analyses**

Factor analysis has become widely applied in ecology and systematics. For instance, randomly generated data have been analyzed and "interpreted" through factor analysis (Armstrong and Soelberg 1968). In addition to the issue of meaningful interpretation, users of factor analysis techniques need also to address the issue of suitability of data and research design. For those engaged in evaluating or planning factor analysis studies, especially those with concern for budgetary or temporal constraints on data collection, a major consideration is the sampling effort necessary to produce data adequate to support a factor analysis. In this context, sample size and number of variables measured become important parameters. The relationship of these parameters to the probability of obtaining at least one principal component from the data has been addressed by Bartlett (1950, 1951). Bartlett's test of sphericity, a significance test of the correlation matrix, can indicate if at least one principal component can be extracted from the data. The test is considered quite powerful, and its routine application is recommended (Knapp and Swoyer 1967; Tobias and Carlson 1969).

Bartlett's test relates sample size ( $N$ ), the determinant of the correlation matrix ( $|R|$ ), and the number of variables measured ( $P$ ) to the  $\chi^2$  distribution ( $df = 0.5(P)(P - 1)$ ) at a given  $\alpha$  through the formula:

$$\chi^2 = - \left[ \frac{N - (2P + 1)}{6} \right] \log_e |R|$$

If the null hypothesis ( $H_0$ ) that no correlation exists among the variables is not rejected, principal component analysis may not be justified. If  $H_0$  is rejected, the existence of at least one principal component is indicated.

By using MDCHI, the IMSL (1975) inverse chi-square subroutine, I have produced curves which show the relationship of the components of Bartlett's test ( $N$ ,  $P$ ,  $|R|$ ) at  $\alpha = 0.01$  and  $0.10$  (Fig. 1). A given curve is a section through the surface defining the smallest  $N$ , largest  $P$ , and largest  $|R|$  (hence, the smallest correlation among variables) possible for statistical significance at a given  $\alpha$ .

The availability of these curves should facilitate the design and evaluation of research involving factor analysis. With information from prior research or subjective estimates, one can use the curves to estimate necessary sample size, statistical significance of a potential factor solution, and the impact of the number of variables to be measured upon the statistical significance of the potential factor solution.

For example, in planning a principal components study of habitat structure, 10 variables of interest are identified. If these are strongly correlated, then  $|R|$  will be low; let  $|R| = 0.3$ . In this case, 50-60 samples need to be taken in order to have a reasonable chance ( $0.1 \leq \alpha \leq 0.10$ ) of justifiably obtaining at least one principal component from the data. If, however, these variables are weakly cor-



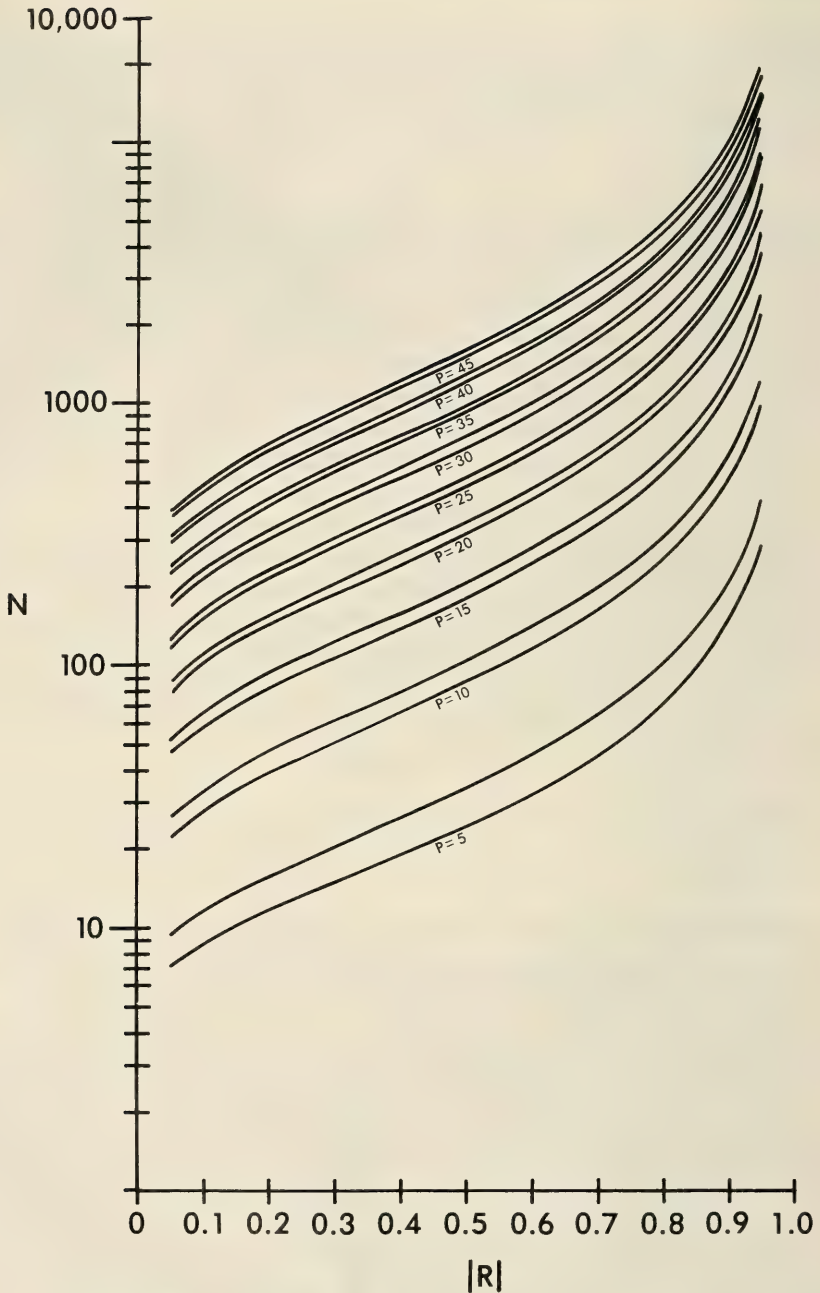


Fig. 1. Limits for statistical significance of principal component analysis as determined by Bartlett's test of sphericity. For each  $P$ , the upper line is set by  $\alpha = 0.01$ ; the lower by  $\alpha = 0.10$ .

related and, let's say,  $|R| = 0.7$ , then an adequate  $N$  would be 150–200, and considerably more effort would be expended in obtaining an adequate sample size.

On the other hand, when sample size is a limiting factor in planning data

collection, reasonable ranges of the number of variables to be studied can be obtained. If a maximum of 50 samples can be collected, it would be unreasonable to expect to justifiably extract principal components from a set of 15 variables unless they were very highly correlated ( $|R| \leq 0.1$ ). If moderate correlations ( $0.2 \leq |R| \leq 0.7$ ) are anticipated, 5–10 variables could reasonably be expected to produce at least one principal component.

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## Notes on the Spawning Cycles of *Labrisomus philippii* (Labrisomidae) and *Trachinotus paitensis* (Carangidae) from Perú

Peru has a highly diverse (Chirichigno 1980) but little studied fish fauna. In an effort to add to our knowledge of the biota from this area, we present data on the spawning cycles of two Peruvian fishes. The little known subtropical labrisomid *Labrisomus philippii* extends from Isla Lobos de Tierra, Peru to Coquimbo, Chile (Chirichigno 1980). The tropical carangid *Trachinotus paitensis* has a wider geographic range, extending from Peru to Redondo Beach, southern California (Miller and Lea 1976). Nothing is known about the reproductive biology of either species. The purpose of this note is to provide a histological analysis of ovarian samples collected during summer and winter.

Fifty-eight *T. paitensis* were obtained from the Mercado Pesquero Artesenal de Chorrillos, Chorrillos, Lima, Perú (12°08'S, 77°02'W). Thirty-two were collected during January 1983, 17 during May, and 9 during June 1983. Seventy-eight *L. philippii* were obtained from the same market. Forty-four were from January, 23 from May, and 11 from June.

Fresh fish were weighed to the nearest g and measured to the nearest mm. Ovaries were removed and preserved in 10% formalin and later weighed to the nearest 0.01 g. Gonosomatic indices ( $GSI = \text{ovary weight/fish weight} \times 100$ ) were calculated from measurements made after preservation. Ovaries were embedded in paraffin; histological sections were cut at 8  $\mu\text{m}$  and stained with Harris' hematoxylin followed by eosin counterstain.

*Labrisomus philippii* adult females average 179 mm standard length (SL) and 156 g weight. Females were reproductively active during January. Ovarian classes are given in Table 1. Most females contained mature oocytes. A mature group of oocytes (mean diameter 491  $\mu\text{m}$ ) was typically present along with one smaller vitellogenic mode (accumulating yolk) which measured 294  $\mu\text{m}$  (mean diameter). This suggests *L. philippii* spawns more than once a year. This is further supported by the presence of females (7%) with mature yolk-filled oocytes for a subsequent spawning and postovulatory follicles from a recent spawning. Postovulatory follicles are remnants of the granulosa layer of the spawned egg which hypertrophy. It was determined by Hunter and Goldberg (1980) that the postovulatory follicle has a brief existence in the northern anchovy, *Engraulis mordax* and is indistinguishable from atretic follicles after 48 hours. We noted that approximately one third of the females were in regressed condition. These contained ovaries consisting of primary oocytes. The smallest reproductively active female (mature oocytes present) measured 128 mm SL.

During May-June, 98% of the sample contained regressed ovaries. Both females and males were not as brightly colored as they were during January when reproduction was occurring. Gonosomatic indices (Table 1) for this period were one quarter their January sizes indicating *L. philippii* has a restricted spawning season which ended several months previously. Student's t test was significant for differences in gonosomatic indices between January and May-June ( $t = 5.91$ ,  $P <$

Table 1. Ovarian classes with mean gonosomatic indices ( $\pm$ SE) for *Labrisomus philippii* and *Trachinotus paitensis* from Peru.

| Month                        | N  | Re-gressed (%) | Mature oocytes (%) | Hydrated eggs (%) | Post-ovulatory follicles (%) | Gonosomatic index |
|------------------------------|----|----------------|--------------------|-------------------|------------------------------|-------------------|
| <i>Labrisomus philippii</i>  |    |                |                    |                   |                              |                   |
| January                      | 44 | 30             | 61                 | 2                 | 7                            | $2.81 \pm 0.33$   |
| May-June                     | 34 | 98             | 2                  | 0                 | 0                            | $0.71 \pm 0.10$   |
| <i>Trachinotus paitensis</i> |    |                |                    |                   |                              |                   |
| January                      | 32 | 3              | 82                 | 6                 | 9                            | $3.37 \pm 0.13$   |
| May-June                     | 26 | 19             | 77                 | 4                 | 0                            | $2.98 \pm 0.32$   |

0.001) samples. Besides the single mature (ripe) female in our sample (Table 1), none of the remaining females showed signs of reproductive activity. High frequencies of oocyte atresia are commonly seen at the close of the spawning season when oocytes that initiated, but did not complete, yolk deposition degenerate (Goldberg 1981). No traces of this large scale atresia were noted. Thus, one can speculate that the sample had been reproductively inactive for several months.

Adult female *T. paitensis* average 305 mm SL and 599 g weight. In January, *T. paitensis* was in spawning condition. The majority of females contained mature, yolk-filled oocytes (mean diameter 435  $\mu$ m) (Table 1). This species spawns more than once as vitellogenic (filling with yolk) oocytes (mean diameter 254  $\mu$ m) were present together with mature, yolk-filled oocytes. Some contained ripe, hydrated eggs. Hydration occurs when the mature oocyte grows to as much as four times its original volume prior to spawning (Wallace and Selman 1981). Postovulatory follicles were noted in 9% of the January sample. The smallest reproductively active female (mature oocytes present) was 260 mm SL.

The spawning cycle continued during May-June (Table 1), although at a reduced rate from January. Nineteen percent of this sample was regressed. Student's *t* test was not significant for differences in gonosomatic indices ( $t = 1.14$ ,  $P = 0.25$ ) between January and May-June. It is difficult to predict the duration of the cycle. It may have continued for another month or two as females with incidences of atretic oocytes, normally seen at the close of the spawning cycle (Goldberg 1981), were not observed.

There are no reports of the duration of the *T. paitensis* spawning cycle. However, Finucane (1969) found that *T. carolinus* and *T. falcatus* from Florida had prolonged spawning periods with main spawning occurring April-June and reduced spawning lasting into early fall. As *T. paitensis* extends from Peru to southern California (Miller and Lea 1976), it will be of interest to examine reproductive samples from the northern part of its range for comparative purposes.

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Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 in *Vertebrates of California*. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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COVER: *Helminthoglypta diabloensis* (Cooper), holotype, UCMP 37536. Top, apertural, and basal views,  $\times 1.5$ . From Barry Roth and Eugene V. Coan.